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Phylogeny and classification of Rosaceae

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Abstract. Phylogenetic relationships among 88 genera of Rosaceae were investigated using nucleotide sequence data from six nuclear (18S, *gbssi*1, *gbssi*2, ITS, *pgip*, and *ppo*) and four chloroplast (*mat*K, *ndh*F, *rbc*L, and *trn*L-*trn*F) regions, separately and in various combinations, with parsimony and likelihood-based Bayesian approaches. The results were used to examine evolution of non-molecular characters and to develop a new phylogenetically based infrafamilial classification. As in previous molecular phylogenetic analyses of the family, we found strong support for monophyly of groups corresponding closely to many previously recognized tribes and subfamilies, but no previous classification was entirely supported, and relationships among the strongly supported clades were weakly resolved and/or conflicted between some data sets. We recognize three subfamilies in Rosaceae: Rosoideae, including *Filipendula*, *Rubus*, *Rosa*, and three tribes; Dryadoideae, comprising the four actinorhizal genera; and Spiraeoideae, comprising *Lyonothamnus* and seven tribes. All genera previously assigned to Amygdaloideae and Maloideae are included in Spiraeoideae. Three supertribes, one in Rosoideae and two in Spiraeoideae, are recognized.

Key words: Rosodae, Pyrodae, Kerriodae, chromosome number, fruit type.

Introduction

In spite of general familiarity with and interest in the family, phylogenetic relationships among taxa within Rosaceae have remained poorly understood and to date no infrafamilial classification has been proposed that recognizes only groups strongly supported as monophyletic. Moreover, although the approximately 90 genera and 3,000 species that are now generally accepted as belonging to the family have long been included in it, circumscription of Rosaceae, in terms of the inclusion or exclusion of other taxa, has varied among the major treatments of the family proposed over the last 60 years (Potter 2003). Taxa currently assigned to families Chrysobalanaceae (Malpighiales), Neuradaceae (Malvales), and Quillajaceae (Fabales) (Morgan et al. 1994, Angiosperm Phylogeny Group 2003) were all at one time included within Rosaceae (e.g. Lawrence 1951, Hutchinson 1964), the last as recently as Takhtajan's (1997) treatment of the family. The single species of *Apopetalum* Pax, listed in tribe Spiraeeae by Hutchinson (1964), was later determined (Cuatrecasas 1970) to be a species of *Brunellia* (Brunelliaceae, Oxalidales). Most recently, Oh and Potter (2006) showed that *Guamatela* Donn. Sm., previously classified in tribe Neillieae of Rosaceae (Hutchinson 1964), is most closely related to species in the order Crossosomatales.

Molecular phylogenetic studies (Morgan et al. 1994, Evans et al. 2000, Potter et al. 2002) have provided strong support for monophyly of Rosaceae. Despite a long tradition of grouping these genera together, there is no readily identifiable morphological synapomorphy for the family. Presence of an hypanthium and reduction or lack of endosperm are both probably synapomorphies for the order Rosales, and hence symplesiomorphies of Rosaceae (Judd and Olmstead 2004). Numerous stamens is a possible synapomorphy for the family (Judd and Olmstead 2004); if so, stamen number has been secondarily reduced several times within Rosaceae.

The position of Rosaceae with respect to other angiosperm families has varied among taxonomic treatments over the last century and has been substantially affected by recent molecular phylogenetic studies. Besides Chrysobalanaceae and/or Neuradaceae, which, as mentioned above, were sometimes included within Rosaceae, previous treatments have included in Rosales Saxifragaceae, Crassulaceae, and Cunoniaceae (e.g., Cronquist 1981) or Dichapetalaceae and Calycanthaceae (Hutchinson 1964), none of which molecular evidence supports as being particularly closely related to Rosaceae. The current circumscription of Rosales (Angiosperm Phylogeny Group 2003) includes Barbeyaceae, Cannabaceae, Dirachmaceae, Elaeagnaceae, Moraceae, Rhamnaceae, Rosaceae, Ulmaceae, and Urticaceae. Molecular evidence indicates that Rosaceae are sister to the remaining families in the order (Soltis et al. 2000, Potter 2003, Judd and Olmstead 2004).

Classification within Rosaceae also varies considerably among treatments (Table 1). The most widely adopted classification (Schulze-Menz 1964) is primarily based on fruit type and has four subfamilies, which are further divided into tribes and subtribes. Hutchinson (1964), on the other hand, recognized only tribes and did not group these into subfamilies. Takhtajan (1997), incorporating some of the results of the first molecular phylogenetic study of relationships across Rosaceae (Morgan et al. 1994), recognized twelve subfamilies. In Takhtajan's treatment, Amygdaloideae and Maloideae were expanded, and Rosoideae and Spiraeoideae were subdivided, as compared to earlier classifications. The treatment of Rosaceae by C. Kalkman, published posthumously by Kubitzki (2004, Kalkman 2004), recognizes only tribes within Rosaceae. Kalkman, however, suggested the possibility of recognizing two subfamilies, one comprising the classical Rosoideae and Prunoideae (hereafter, Amygdaloideae), the other the classical Maloideae and Spiraeoideae. This would represent a rather different treatment than the one adopted here, in which the circumscription of Rosoideae is narrower than in most previous treatments, Dryadoideae is recognized as a separate subfamily, and Spiraeoideae is expanded to include the classical Amygdaloideae and Maloideae. Kalkman's treatment includes more comprehensive surveys of vegetative and reproductive morphology, karyology, reproductive behavior, ecology, phytochemistry, economic uses, and conservation issues than is possible here. In addition to the tribes adopted from earlier treatments, Kalkman designated three informal groups around the genera *Alchemilla*, *Geum*, and *Cydonia* (Table 1). *Adenostoma*, *Coleogyne*, *Potaninia*,

Table 1. Comparison of the new classification for Rosaceae presented here with four previously published classifications of the family. Parentheses around a group of generic names within a column indicates that, in that treatment, those genera were included in the genus listed directly above them. A notation of — indicates that the genus was not mentioned in the treatment, or, in the case of this paper, that the genus has not been represented in any phylogenetic study of the family to date. Superscripts are used as follows: Letters indicate cases in which differences in placement of a genus in different treatments precluded the possibility of aligning them in the table; Roman and Arabic numerals, respectively, indicate cases in which tribes and subfamilies had to be split within a treatment. Taxonomic authorities for supertribes, tribes, subtribes, and genera are included in the taxonomic treatment section of the Discussion

This Paper	**Schulze-Menz (1964)**	**Hutchinson (1964)**	**Takhtajan (1997)**	**Kalkman (2004)**
Rosoideae	Rosoideae^{I}		Fillpenduloideae	
	Ulmarieae	Ulmarieae		Ulmarieae
Filipendula	*Filipendula*	*Filipendula*	*Filipendula*	*Filipendula*
			Rosoideae	
Rosodae				
	Roseae	Roseae		Roseae
Rosa	*Rosa*	*Rosa*	*Rosa*	*Rosa*
(Hulthemia)	*(Hulthemia)*	*(Hulthemia)*	*Hulthemia*	*(Hulthemia)*
	Rubeae	Rubeae	Ruboideae	Rubeae
Rubus	*Rubus*	*Rubus*	*Rubus*	*Rubus*
(Dalibarda)	*Dalibarda*	*(Dalibarda)*	*(Dalibarda)*	
			Potentilloideae	
Sanguisorbeae	Sanguisorbeae	Poterieae	Sanguisorbeae	Sanguisorbeae
Agrimoniinae	Agrimoniinae			
Agrimonia	*Agrimonia*	*Agrimonia*	*Agrimonia*	*Agrimonia*
Aremonia	—	*Aremonia*	*Aremonia*	*Aremonia*
Hagenia	*Hagenia*	*Hagenia*	*Hagenia*	*Hagenia*
Leucosidea	—	*Leucosidea*	*Leucosidea*	*Leucosidea*
Spenceria	—	*Spenceria*	*Spenceria*	*Spenceria*
Sanguisorbinae	Sanguisorbinae			
Acaena	*Acaena*	*Acaena*	*Acaena*	*Acaena*
Cliffortia	*Cliffortia*	*Cliffortia*	*Cliffortia*	*Cliffortia*
Margyricarpus	*Margyricarpus*	*Margyricarpus*	*Margyricarpus*	*Margyricarpus*
(Tetraglochin)	—	*Tetraglochin*	*Tetraglochin*	(*Tetraglochin*)
Polylepis	*Polylepis*	*Polylepis*	*Polylepis*	*Polylepis*
Sanguisorba	*Sanguisorba*	*Sanguisorba*	*Sanguisorba*	*Sanguisorba*
Poteridium	—	*Poteridium*	—	(*Poteridium,*
Poterium	*Poterium*	*Poterium*	—	*Poterium*)
(Bencomia,	—	*Bencomia*	*Bencomia*	*Bencomia*

Table 1. (Continued)

This Paper	Schulze-Menz (1964)	Hutchinson (1964)	Takhtajan (1997)	Kalkman (2004)
Marcetella,	—	—	—	*Marcetella*,
Dendriopoterium,	—	—	—	*Dendriopoterium)*
Sarcopoterium)	—	*Sarcopoterium*	*Sarcopoterium*	*Sarcopoterium*
see below[a]	see below[a]	*Alchemilla*[a]	see below[a]	see below[a]
Potentilleae	Potentilleae	Potentilleae	Potentilleae	Potentilleae
	Potentillineae			
Potentilla	*Potentilla*	*Potentilla*	*Potentilla*	*Potentilla*
(*Argentina*,	—	*Argentina*	—	—
Comarella,	—	*Comarella*	—	*(Comarella*,
Duchesnea,	*Duchesnea*	*Duchesnea*	*Duchesnea*	*Duchesnea*,
Horkelia,	*Horkelia*	*Horkelia*	*Horkelia*	*Horkelia*,
Horkeliella,	—	*Horkeliella*	*Horkeliella*	*Horkeliella*,
Ivesia,	*Ivesia*	*Ivesia*	*Ivesia*	*Ivesia*,
Purpusia,	—	*Purpusia*	—	*Purpusia*,
Stellariopsis)	—	*Stellariopsis*	—	*Stellariopsis*
Fragariinae	Alchemillinae			
Comarum	*Comarum*	*Comarum*	*Comarum*	*Comarum*,
(*Farinopsis*)	—	—	—	—
Dasiphora	—	*Pentaphylloides*	—	—
Drymocallis	—	*Drymocallis*	—	*Drymocallis*,
Sibbaldia	—	*Sibbaldia*	*Sibbaldia*	*Sibbaldia*,
Sibbaldiopsis	—	*Sibbaldiopsis*	—	*Sibbaldiopsis)*
Chamaerhodos	—	*Chamaerhodos*	*Chamaerhodos*	*Chamaerhodos*
Fragaria	*Fragaria*	*Fragaria*	*Fragaria*	*Fragaria*
			Alchemilleae	*Alchemilla* Group
Alchemilla	*Alchemilla*	see above[a]	*Alchemilla*	*Alchemilla*
(*Aphanes*,	*Aphanes*	—	*Aphanes*	*(Aphanes*,
Lachemilla,	*Lachemilla*	—	—	*Lachemilla*,
Zygalchemilla)	—	—	—	*Zygalchemilla)*
				unclear tribal position
Potaninia[b]	—	see below[b]	see below[b]	*Potaninia*[b]
Sibbaldianthe	—	—	—	—
(Schistophyllidium)	—	—	—	—
Colurieae	Dryadeae	Dryadeae	Geeae	*Geum* Group
	Geinae			
Geum	*Geum*	*Geum*	*Geum*	*Geum*

(Acomastylis,	*(Acomastylis,*	*Acomastylis*	—	*Acomastylis*
Novosieversia,	—	*Novosieversia*	*Novosieversia*	*(?Novosieversia)*
Oncostylus,	*Oncostylus)*	—	—	*Oncostylus*
Orthurus,	—	*Orthurus*	*Orthurus*	*Orthurus*
—	—	—	—	*Parageum*
Taihangia,	—	—	*Taihangia*	*(?Taihangia)*
Coluria,	*Coluria*	*Coluria*	*Coluria*	*Coluria*
				Doubtfully in *Geum* Group
Waldstenia)	*Waldsteinia*	*Waldsteinia*	*Waldsteinia*	*Waldsteinia*
Sieversia	—	*Sieversia*	*Sieversia*	*Sieversia*
	Dryadinae		Dryadeae	
Fallugia	*Fallugia*	*Fallugia*	*Fallugia*	*Fallugia*
Dryadoideae				
				Dryadeae
Dryas	*Dryas*	*Dryas*	*Dryas*	*Dryas*
	Purshiinae		Purshieae	
Chamaebatia	*Chamaebatia*	*Chamaebatia*	*Chamaebatia*	*Chamaebatia*
Purshia	*Purshia*	*Purshia*	*Purshia*	*Purshia*
(Cowania)	*Cowania*	*Cowania*	*Cowania*	*Cowania*
	Cercocarpinae	Cercocarpeae	Cercocarpeae	
Cercocarpus	*Cercocarpus*	*Cercocarpus*	*Cercocarpus*	*Cercocarpus*
			Potaninieae	
see above^{b}	—	*Potaninia*^{b}	*Potaninia*^{b}	see above^{b}
see below^{c}	see below^{c}	*Coleogyne*^{c}	see below^{c}	see below^{c}
Spiraeoideae	Lyonothamnoideae			
		Quillajeae^{2}		unclear tribal position
Lyonothamnus^{d}	see below^{d}	*Lyonothamnus*^{d}	*Lyonothamnus*^{d}	*Lyonothhamnus*^{d}
Kerriodae				
			Coleogynoideae	
Kerrieae	Kerrieae	unclear tribal position		
Coleogyne	*Coleogyne*	see above^{c}	*Coleogyne*	*Coleogyne*
			Kerrioideae	
		Kerrieae	Kerrieae	Kerrieae
Kerria	*Kerria*	*Kerria*	*Kerria*	*Kerria*
Neviusia	*Neviusia*	*Neviusia*	*Neviusia*	*Neviusia*
		Rhodotypeae	Rhodotypeae	
Rhodotypos	*Rhodotypos*	*Rhodotypos*	*Rhodotypos*	*Rhodotypos*

Table 1. (Continued)

This Paper	Schulze-Menz (1964)	Hutchinson (1964)	Takhtajan (1997)	Kalkman (2004)
	Spiraeoideae[II]		Amygdaloideae	
Osmaronieae	Exochordeae[1]	Quillajeae[2]	Exochordeae	Exochordeae[3]
Exochorda	*Exochorda*	*Exochorda*	*Exochorda*	*Exochorda*
	Prunoideae			
		Osmaronieae	Osmaronieae	Pruneae
Oemleria	*Oemleria*	*Oemleria* (as *Osmaronia*)	*Oemleria*	*Oemleria*
		Pruneae		Prinsepieae
Prinsepia	*Prinsepia*	*Prinsepia*	*Prinsepia*	*Prinsepia*
(Plagiospermum)	—	*Plagiospermum*	—	*(Plagiospermum)*
Amygdaleae	Amygdaleae			
Prunus	*Prunus*	*Prunus*	*Prunus*	*Prunus*
(Armeniaca,	*(Armeniaca,*	*(Armeniaca,*	*Armeniaca*	—
Cerasus,	*Cerasus,*	*Cerasus)*	*Cerasus*	*(Cerasus,*
Amygdalus,	*Amygdalus,*	*Amygdalus*	*Amygdalus*	*Amygdalus,*
Padus,	*Padus,*	*Padus*	*Padus*	*Padus,*
Laurocerasus,	*Laurocerasus)*	*Laurocerasus*	*Laurocerasus*	*Laurocerasus,*
Pygeum,	*Pygeum*	*Pygeum*	*Pygeum*	*Pygeum)*
Maddenia)	*Maddenia*	*Maddenia*	*Maddenia*	*Maddenia*
	Rosoideae[I]		Spiraeoideae	
Sorbarieae	Adenostomeae	Adenostomateae	Adenostomateae	unclear tribal position
Adenostoma	*Adenostoma*	*Adenostoma*	*Adenostoma*	*Adenostoma*
	Spiraeoideae[II]			
	Sorbarieae	Gillenieae[4]	Sorbarieae	Gillenieae[4]
Sorbaria	*Sorbaria*	*Sorbaria*	*Sorbaria*	*Sorbaria*
Chamaebatiaria	*Chamaebatiaria*	*Chamaebatiaria*	*Chamaebatiaria*	*Chamaebatiaria*
see above[d]	*Lyonothamnus*[d]	See above[d]	see above[d]	see above[d]
Spiraeanthus[e]	see below[e]	*Spiraeanthus*[e]	see below[e]	*Spiraeanthus*[e]
Spiraeeae	Spiraeeae	Spiraeeae	Spiraeeae	Spiraeeae
Aruncus	*Aruncus*	*Aruncus*	*Aruncus*	*Aruncus*
Kelseya	—	*Kelseya*	*Kelseya*	*Kelseya*
Luetkea	—	*Luetkea*	*Luetkea*	*Luetkea* (as *Eriogynia)*
Petrophyton	—	*Petrophyton*	*Petrophyton*	*Petrophyton* (as *Petrophytum*)
Sibiraea	*Sibiraea*	*Sibiraea*	*Sibiraea*	*Sibiraea*
Spiraea	*Spiraea*	*Spiraea*	*Spiraea*	*Spiraea*

—	—	(*Pentactina*)	*Pentactina*	(*Pentactina*)
Xerospiraea	—	—	—	*Xerospiraea*
	Holodisceae	Holodisceae	Holodisceae	
Holodiscus	*Holodiscus*	*Holodiscus*	*Holodiscus*	*Holodiscus*
Neillieae	Neillieae	Neilieae	Neillieae	Neillieae
Physocarpus	*Physocarpus*	*Physocarpus*	*Physocarpus*	*Physocarpus*
Neillia	*Neillia*	*Neillia*	*Neillia*	*Neillia*
(*Stephanandra*)	*Stephanandra*	*Stephanandra*	*Stephanandra*	*Stephanandra*
Pyrodae	Gillenieae	Gillenieae[4]	Gillenieae	Gillenieae[4]
Gillenia Moench.	*Gillenia*	*Gillenia* (as *Porteranthus*)	*Gillenia*	*Gillenia*
see above[e]	*Spiraeanthus*[e]	See above[e]	*Spiraeanthus*[e]	see above[e]
			Pyroideae	
Pyreae	Quillajeae[2]	Quillajeae[2]	Kageneckieae	Exochordeae[3]
Kageneckia	*Kageneckia*	*Kageneckia*	*Kageneckia*	*Kageneckia*
			Lindleyieae	
Vauquelinia	*Vauquelinia*	*Vauquelinia*	*Vauquelinia*	*Vauquelinia*
	Exochordeae[1]			
Lindleya	*Lindleya*	*Lindleya*	*Lindleya*	*Lindleya*
Pyrinae	Maloideae			
	Maleae	Pomeae	Maleae	Maleae[5]
Amelanchier	*Amelanchier*	*Amelanchier*	*Amelanchier*	*Amelanchier*
Malacomeles	—	*Malacomeles*	*Malacomeles*	(*Malacomeles*,
Peraphyllum	—	*Peraphyllum*	*Peraphyllum*	*Peraphyllum*)
Aronia	—	*Aronia*	*Aronia*	*Aronia*
Photinia	*Photinia*	*Photinia*	*Photinia*	(*Photinia*)
Docyniopsis	—	—	*Docyniopsis*	*Macromeles*
Eriobotrya	*Eriobotrya*	*Eriobotrya*	*Eriobotrya*	*Eriobotrya*
Eriolobus	—	*Eriolobus*	*Eriolobus*	*Eriolobus*
Heteromeles	—	—	*Heteromeles*	*Heteromeles*
Malus	*Malus*	*Malus*	*Malus*	*Malus*
Stranvaesia	*Stranvaesia*	*Stranvaesia*	(*Stranvaesia*)	(*Stranvaesia*)
Pyrus	*Pyrus*	*Pyrus*	*Pyrus*	*Pyrus*
Rhaphiolepis	*Rhaphiolepis*	*Rhaphiolepis*	*Rhaphiolepis*	*Rhaphiolepis*
Sorbus	*Sorbus*	*Sorbus*	*Sorbus*	*Sorbus*
Aria	—	—	—	(*Aria*,
Chamaemespilus	—	—	*Chamaemespilus*	*Chamaemespilus*,
Cormus	—	—	*Cormus*	*Cormus*,
Torminalis	—	—	*Torminalis*	*Torminalis*)

Table 1. (Continued)

This Paper	Schulze-Menz (1964)	Hutchinson (1964)	Takhtajan (1997)	Kalkman (2004)
				Cydonia Group
Chaenomeles	*Chaenomeles*	*Chaenomeles*	*Chaenomeles*	*Chaenomeles*
Cydonia	*Cydonia*	*Cydonia*	*Cydonia*	*Cydonia*
Docynia	—	*Docynia*	*Docynia*	*Docynia*
Pseudocydonia	—	*Pseudocydonia*	*Pseudocydonia*	*Pseudocydonia*
	Crataegeae	Crataegeae		Crataegeae
Chamaemeles	—	*Chamaemeles*	*Chamaemeles*	*Chamaemeles*
Cotoneaster	*Cotoneaster*	*Cotoneaster*	*Cotoneaster*	*Cotoneaster*
Crataegus	*Crataegus*	*Crataegus*	*Crataegus*	*Crataegus*
Hesperomeles	—	*Hesperomeles*	*Hesperomeles*	*Hesperomeles*
Mespilus	*Mespilus*	*Mespilus*	*Mespilus*	*Mespilus*
Osteomeles	—	*Osteomeles*	*Osteomeles*	*Osteomeles*
Pyracantha	*Pyracantha*	*Pyracantha*	*Pyracantha*	*Pyracantha*
			Dichotomanthoideae	Maleae[5]
Dichotomanthes	—	*Dichotomanthes*	*Dichotomanthes*	*Dichotomanthes*

and *Lyonothamnus* were not assigned to tribes. Both *Guamatela* and *Brachycaulos* Dikshit & Panagrahi are listed as "doubtfully Rosaceaous." The latter genus is known only from a single collection from India (Kalkman 2004) and will not be considered further in this paper.

Studies of phylogenetic relationships within Rosaceae based upon molecular data have agreed in providing strong support for several clades that more or less correspond to previously recognized subfamilies and tribes and in showing rather weak support for the relationships among those clades. Morgan et al.'s (1994) phylogenetic analysis of *rbc*L sequence variation across the family resolved as monophyletic groups that corresponded, with a fair number of modifications, to Schulze-Menz's (1964) Rosoideae, Amygdaloideae, and Maloideae, but Spiraeoideae were polyphyletic. The results suggested that, in Rosaceae, chromosome number is a better indicator of relationship than is fruit type. Taxa with $x = 9$ traditionally assigned to Rosoideae because their members produce achenes were found to fall outside of Rosoideae *sensu stricto* ($x = 7$, 8), whereas several taxa with $x = 15$ and 17 traditionally classified in Spiraeoideae because they produce follicles were found to be more closely related to pome-bearing Maloideae. *Prunus* ($x = 8$, drupes) was weakly supported as sister to a strongly supported clade of three other genera with the same base chromosome number; members of two of those genera (*Oemleria* and *Prinsepia*) also bear drupes, but those of the third, *Exochorda*, produce capsules (more accurately, cocceta; see Results).

Analyses of chloroplast *ndh*F sequences (Evans 1999) and morphological and ontogenetic characters (Evans 1999; Evans and Dickinson 1999a, 1999b) provided support for many of the clades that were also strongly supported by Morgan et al.'s (1994) study. Potter et al.'s (2002) analyses of chloroplast *mat*K and *trn*L-*trn*F sequences also resolved most of these clades but differed in details of the relationships among them, though most of those relationships were not well supported by any of the analyses. One important difference concerned relationships among basally diverging lineages in the family. The *rbc*L data provided weak support for a sister relationship between Rosoideae *sensu stricto* and the rest of the family, while in the strict consensus tree based on *mat*K and *trn*L-*trn*F data, three clades formed an unresolved polytomy diverging at the base of the family: Rosoideae *sensu stricto*, the actinorhizal taxa (Dryadoideae in column 1 of Table 1), and the rest of the family (Spiraeoideae in column 1 of Table 1). Within the last clade, there was strong support for a sister relationship between *Lyonothamnus* and the remaining taxa.

Studies of granule-bound starch synthase gene (*gbssi*) sequences by Evans et al. (2000) and Evans and Campbell (2002) were aimed primarily at investigating the origins of Maloideae. This group has long attracted the attention of evolutionary biologists because of the possibility that it may represent a higher-level angiosperm group of hybrid origin, as suggested by chromosome numbers and isozyme data (Chevreau et al. 1985, Chevreau and Laurens 1987, Weeden and Lamb 1987, Raspé et al. 1998). A particularly intriguing hypothesis holds that the base chromosome number of $x = 17$ in this group resulted from wide hybridization between an ancestral amygdaloid with $x = 8$ and an ancestral spiraeoid with $x = 9$ (Sax 1933). Data from the low copy nuclear gene *gbssi* provide an excellent tool to test this hypothesis. This gene has undergone a duplication prior to the evolution of Rosaceae (Evans et al. 2000), with two copies found in all diploid taxa with $x = 7$, 8, or 9, and another duplication (as a result of ancient polyploidization) within Rosaceae, resulting in four copies in diploid taxa with $x = 15$ or 17. Phylogenetic analyses of these genes for a broad sampling of taxa with the different chromosome numbers from across the family (Evans and Campbell 2002) did not support the wide-hybridization hypothesis. Instead, both *gbssi*1 and *gbssi*2 resolved *Gillenia* ($x = 9$) as sister to the clade including taxa with $x = 15$ or 17, a result also supported by the *ndh*F (Evans 1999) and *mat*K/*trn*L-*trn*F (Potter et al. 2002) data; *Gillenia* was not sampled by Morgan et al. (1994). These results are consistent with a spiraeoid origin of Maloideae (Sterling 1966, Gladkova 1972), and they support an alternative to the wide-hybridization hypothesis, which holds that the higher chromosome number of maloids arose via hybridization and polyploidization among closely related species of an ancestral lineage (the lineage that also gave rise to *Gillenia* with $x = 9$), followed by aneuploid reduction. The results further suggest a New World origin of this group, since *Gillenia*, *Lindleya*, and *Vauquelinia* are all distributed in North America, and *Kageneckia* is found in South America. Finally, these results support recognition of a taxon (here designated supertribe Pyrodae; Table 1) including not only all genera with chromosome numbers of 15 and 17 (Takhtajan's (1997) Pyroideae, our Pyreae; Table 1) but also *Gillenia* with $x = 9$. Outside of this expanded maloid group, the *gbssi* results (Evans and Campbell 2002) resolved several of the same groups of genera that were identified in other molecular phylogenetic studies of the family (Morgan et al. 1994, Evans 1999, Potter et al. 2002) but, once again, provided generally weak resolution of relationships among those groups.

The objectives of the present study are to 1) assemble molecular phylogenetic data for Rosaceae which have been generated in several labs in North America and Europe over the last 10–15 years; 2) analyze these data separately and in combination in order to determine the extent to which different data sets may conflict with one another and to obtain the best hypotheses of phylogenetic relationships in the family according to currently available evidence; 3) explore the implications of the phylogenetic trees generated from molecular data for the evolution of structural, biochemical, and ecological characters; and 4) produce a new, phylogenetically based infrafamilial classification for Rosaceae.

Materials and methods

Data. Ten genes or genomic regions were analyzed in this study (Table 2), including six nuclear and four chloroplast loci. The six nuclear loci are: 18S ribosomal RNA genes, internal transcribed spacer (ITS) regions (including ITS 1, the 5.8S ribosomal RNA gene, and ITS 2), *gbssi*1 and *gbssi*2, and putative genes encoding polygalacturonase inhibitor proteins (PGIP) and polyphenol oxidase (PPO). The four chloroplast loci are: *rbc*L, *mat*K, *ndh*F, and *trn*L-*trn*F.

The taxa sampled for each locus are listed in Table 2. Many of the sequences used in this study were included in previously published analyses; for those that were not, voucher specimen information is given in Table 2, or, for genera of Pyreae, in Campbell et al. (2007). Methods for DNA extraction, PCR amplification, cloning (where necessary) and sequencing of particular loci may be found in the publications listed in Table 2. Data from several loci are published here for the first time, and the methods for PCR and sequencing of these regions are described briefly below.

18S: GenBank 18S sequence of *Prunus persica* (L28749), *Spiraea* x *vanhoutei* (U42801), and *Photinia fraseri* (U42800) were used to design a forward (18S1F: GACTGTGAAACTGCGAATGGCTC) and a reverse PCR primer (18S2R: GTTCACC TACGGAAACCTTGTTACG) as well as two internal primers (18S3F: TAACGAGGATCCA TTGGAGG and 18S4R: AGATCCACCAAC TAAGAACG), which were purchased from Sigma Genosys, Inc. and Integrated DNA Technologies, Inc. Approximately 1.6 kb of the 18S gene were amplified from extracted genomic DNA of each taxon in 25 μl reactions containing 2.5 μL of 100X bovine serum albumin (BSA), 2.5 μL of 10X polymerase buffer, 3 μL of 25 mM $MgCl_2$, 0.5 μL of 10 mM dNTPs, 0.75 μL of each 10 mM primer, 1.0 unit of Taq DNA polymerase (mostly from Promega Inc.), and 15–60 ng of genomic DNA. PCR conditions were as follows: 30 cycles of 94°C for 1.5 min, 55°C for 2 min, and 72°C for 2 min, followed by 72°C for 15 min. PCR products were purified from agarose gels with the Qiaquick Gel Extraction Kit (Qiagen Inc.). PCR products were sequenced directly in both directions using both external and internal primers on an ABI/Prism 377 automated sequencer at the University of Maine DNA Sequencing Facility.

pgip: Sequences of PGIPs from several eudicots (*Malus domestica*, Yao et al. 1995; *Phaseolus vulgaris* L., Toubart et al. 1992; *Actinidia deliciosa* (A. Chev.) Liang and A. R. Ferg., Simpson et al. 1995; *Pyrus communis*, Stotz et al. 1993; and *Lycopersicon esculentum* Miller, Stotz et al. 1994) were obtained from GenBank, aligned, and used to design two forward (PGIP1: TCCTCCTACAAATCAAGAAAG and PGIP5: CCAGCTCTCTCTGATCTCTGCAACCC) and two reverse PCR primers (PGIP2: TTGCAGCTTGGGAGTGGAG and PGIP6: ACCACACAGCCTGTTGTAGCTCAC) as well as two internal sequencing primers (PGIP3: GACCGTAATAAGCTCACAGG and PGIP4: CCTGTGAGCTTATTACGGTC), which were purchased from Genosys Biotechnologies, Inc. Approximately 0.9 kb of the PGIP gene was amplified from extracted genomic DNA of each taxon using the Perkin-Elmer GeneAmp II kit and various combinations of the PCR primers (some primer combinations did not yield any product for some taxa). PCR conditions were as follows: 1 min at 95°C; 40 cycles of 30 s at 95°C, 1 min at 55°C, and 2 min at 72°C; 7 min at 72°C. PCR products were purified from agarose gels with the Qiaquick Gel Extraction Kit (Qiagen Inc.). PCR products were either sequenced directly in both directions (using both external and internal primers as needed), or first cloned using the Invitrogen Topo-TA Cloning Kit. For cloned PCR products, one to ten colonies were selected from each transformation reaction for sequencing in both directions with universal primers M13 or T7 and M13 Reverse or T3 and internal primers as necessary. Automated sequencing was carried out at one of the two DNA sequencing facilities on the U.C. Davis campus, each of which uses an ABI/Prism 377 automated sequencer.

ppo: Based on a consensus of published cDNA or genomic sequences for PPO genes from various species of Rosaceae (Boss et al. 1995; Chevalier et al. 1999; Haruta et al. 1998, 1999), three forward (PPO1: TAGACAGGAGAAATGTGCTTCTT GG, PPO3: GACCCGTTCGCCTTTGCCAAG CC, and PPO5: ATGACGTCTCTTTCACCT CC GGTAGTCAC) and two reverse (PPO2: CACTTACAAAGCTTCCGGCAAACTC and PPO6: TCCTCCGCCTCAATTTCCTCCAACA) PCR primers were designed to amplify a fragment of about 1.5 kb, including most of the coding region of the gene. Two internal sequencing primers

Table 2. Gene regions (with references to methods for sequencing) and taxa sampled in this study with public database accession numbers. Voucher information is provided in cases where it has not previously been published

Genus	18S (this study; voucher information in Evans 1999 or Evans and Campbell 2002)	*gbssi* (Evans et al. 2000, Evans and Campbell 2002, Smedmark et al. 2003, 2005; Campbell et al. 2006)	ITS (Bortiri et al. 2001, Campbell et al. 1995, Eriksson et al. 1998, 2003; Helfgott et al. 2000; Smedmark and Eriksson 2002; Kerr 2004; Campbell et al. 2006; this study)	*pgip*(this study)	*ppo*(this study)	*mat*K (Potter et al. 2002, Campbell et al. 2006)	*ndh*F (Evans 1999; Campbell et al. 2006; this study; additional voucher information in Evans 1999 and Evans and Campbell 2002)	*rbc*L (Morgan et al. 1994; this study)	*trn*L-*trn*F (Potter et al. 2002; Eriksson et al. 2003; Smedmark and Eriksson 2002; Kerr 2004; Campbell et al. 2006; this study)
Acaena	–	–	*cylindristachya* Ruiz & Pav. AJ512775	–	–	–	–	–	*cylindri.* AJ512780
Adenostoma	*fasciculatum* Hook.& SArn. DQ88363	*fascic.* AF500389	*fascic.*Oh 970424-01 (DAV) DQ88358	*fascic.* Oh 970424-01 (DAV) AF196866	*fascic.* Oh 970424-01 (DAV) DQ851197	*fascic.* AF288095	*fascic.* DQ851497	*sparsifolium* Torr. U06790	*fascic.* AF348535
Agrimonia	–	–	*eupatoria* L. U90798	–	–	–	–	*parviflora* Ait. U06791	*eupatoria* AJ512216
Alchemilla	–	–	*alpina* L. U90816, U90817	–	–	–	–	*mollis* (Buser) Rothm. U06792	*alpina* AJ512217
Amelanchier	–	*bartramiana* (Tausch) Roemer AF285973 – AF285976 DQ874881 DQ874907 DQ874909	*bartram.* U151591	–	–	*bartram.*DQ860450	*bartram.*DQ851498	*alnifolia* Nutt. U06793	*bartram.* DQ863222
Aremonia	–	–	*agrimonioides* (L.) DC. U90799	–	–	–	–	–	*agrimon.* AJ512230, AJ512231
Aria	–	*alnifolia*(Siebold & Zucc.) Decne. AF500390 - AF500393	*alnifolia*U16185	–	–	*alnifolia* DQ860451	*alnifolia* DQ851499	–	*alnifolia* DQ863223
Aronia	–	*arbutifolia*(L.) Elliott AF500394 – AF500395	*arbutifolia* U16199	–	–	*arbutifolia* DQ860452	*arbutifolia* DQ851500	–	*arbutifolia* DQ863224
Aruncus	–	*dioicus*(Walter) Fernald AF285999 – AF286001	–	*dioicus*UC Bot. Gard. 83.0466 AF196868	–	*dioicus* AF288094	*dioicus* UC Bot. Gard. 83.0466 DQ851501	*sylvester* Kostel. U06794	*dioicus* AF348536
Ceanothus	*sanguineus* Pursh. U42799	–	*gloriosus* J. T. Howell AF398524	–	–	–	*americanus* L. DQ851502	*sanguineus* U06795	–

Table 2. (Continued)

Cercocarpus	*betuloides* Nutt. DQ88364	*betuloides* AF500396 – AF500397	*betuloides* Gao s.n. (DAV) DQ88355	*betuloides* Gao s.n. (DAV) AF196870	*betuloides* Gao s.n. (DAV) DQ851198	*betuloides* AF288095	*betuloides* Gao s.n. (DAV) DQ851503	*ledifolius* Nutt. ex Torr. & A. Gray U06796	*betuloides* AF348537
Chaenomeles	–	*speciosa* (Sweet) Nakai AF285977 – AF285979 AF500398 DQ874902	*cathayensis* (Hemsl.) C. K. Schneid. U16186	*speciosa* UCD Arboretum A80.0005 AF196871	*speciosa* UCD Arboretum A80.0005 DQ851199	*cathayensis* DQ860453	*speciosa* DQ851504	–	*cathayensis* DQ863225
Chamaebatia	*foliolosa* Benth. DQ88365	*australis* (Bdg.) Abrams DQ904401	*foliolosa* Potter 970427-02 (DAV) DQ88356	*foliolosa* Potter 970427-02 (DAV) AF196872	*foliolosa* Potter 970427-02 (DAV) DQ851200	*foliolosa* AF288096	*foliolosa* DXP 313 Larson s.n. (DAV) DQ851505	–	*foliolosa* AF348538
Chamaebatiaria	*millefolium* (Torr.) Maxim. DQ88366	*millefolium* AF500399 – AF500400	*millefolium* UCD Arb. A74.0245 DQ88359	*millefolium* UCD Arb. A74.0245 AF196874	*millefolium* UCD Arb. A74.0245 DQ851201	*millefolium* AF288097	*millefolium* DQ851506	*millefolium* U06797	*millefolium* AF348539
Chamaemeles	–	–	*coriacea* Lindley DQ811768	–	–	*coriacea* DQ860454	*coriacea* DQ851507	–	*coriacea* DQ863226
Chamaemespilus	–	*alpina* (Miller) Robertson & Phipps AF500401 – AF500404	*alpina* DQ811769	–	–	*alpina* DQ860455	*alpina* DQ851508	–	*alpina* DQ863227
Chamaerhodos	–	–	*erecta* (L.) Bunge U90794	–	–	–	–	–	*erecta* AJ512219
Cliffortia	–	–	*odorata* L.f. AY634874	–	–	–	–	–	*odorata* AY634724
Coleogyne	–	–	–	–	–	*ramosissima* Torr. Potter 020913-01 (DAV) DQ851224	–	–	–
Comarum	–	–	*palustre* L. AJ511777	–	–	–	–	–	*palustre* AJ512237
Cormus	–	*domestica* Spach AF500405 - AF500408	*domestica* U16187	–	–	*domestica* DQ860456	*domestica* DQ851509	–	*domestica* DQ863228
Cotoneaster	–	*lacteus* W. W. Smith AF500409 - AF500412	*lacteus* U16188	–	–	*lacteus* DQ860457	*apiculatus* Rehd. & Wilson DQ851510	–	*lacteus* DQ863229
Cowania	–	–	–	–	–	–	–	*stansburiana* Torr. U59817	–
Crataegus	–	*rivularis* Nutt. AF500413 - AF500414 DQ874883	*mollis* Scheele U16190	*monogyna* Jacq. Potter 970517-08 (DAV) AF196879	*monogyna* Potter 970517-08 (DAV) DQ851202	*submollis* Sarg. DQ860458	*rivularis* DQ851511	*columbiana* Howell U06799	*submollis* DQ863230
Cydonia	–	*oblonga* Miller AF500415 - AF500416 DQ874910	*oblonga* U16189	–	–	*oblonga* DQ860459	*oblonga* DQ851512	–	*oblonga* DQ863231

Dasiphora	–	–	*fruticosa* (L.)Rydb. U90808, U90809	*fruticosa* cultivar J. Luby s.n. AF196918	*fruticosa* cultivar J. Luby s.n. DQ851214	–	*fruticosa* DQ851513	*fruticosa* U06818	*fruticosa* AJ512233
Dichotomanthes	–	*tristaniicarpa* Kurz AF500417 - AF500420	*tristaniicarpa* DQ811770	–	–	*tristaniicarpa* DQ860460	*tristaniicarpa* DQ851514	–	*tristaniicarpa* DQ863232
Docyniopsis	–	*tschonskii* (Maxim.) Koidzumi AF500421 - AF500422 DQ874884	*tschonskii* DQ811771	–	–	*tschonskii* DQ860461	*tschonskii* DQ851515	–	*tschonoskii* DQ863233
Dryas	–	*octopetala* L. Smedmark 11 (S) AM116868	*octopetala* U90804	–	–	*octopetala* Potter 011020-01 (DAV) DQ851225	*octopetala* Potter 011020-01 (DAV) DQ851516	*drummondii* Richards. ex Hook. U59818	*octopetala* Potter 011020-01 (DAV) DQ851231
Drymocallis	–	–	*agrimonioides* (Pursh) Rydb. U90787	–	–	–	–	–	*agrimonioides* AJ512223
Eriobotrya	–	*japonica* Lindl. AF500423 - AF500424 DQ874901	*japonica* U16192	–	–	*japonica* DQ860462	*japonica* DQ851517	*japonica* U06800	*japonica* DQ863234
Eriolobus	–	*trilobata* Roemer AF500425 - AF500428	–	–	–	*trilobata* DQ860463	*trilobata* DQ851518	–	*trilobata* DQ863235
Exochorda	*racemosa* (Lindl.) Rehder DQ88367	*racemosa* AF286002 - AF286003	*racemosa* AF318740	*racemosa* UCD Arb. AF196885	*racemosa* UCD Arb. DQ851203	*racemosa* AF288100	*racemosa* DQ851519	*giraldii* Hesse U06801	*racemosa* AF348542
Fallugia	–	*paradoxa* Endl. AJ871485 T. Eriksson 796 (SBT) AM116868	*paradoxa* U90805	–	*paradoxa* Potter 970428-01 (DAV) DQ851204	*paradoxa* AF288101	*paradoxa* Potter 970428-01 (DAV) DQ851520	*paradoxa* U06802	*paradoxa* AJ297331
Filipendula	*vulgaris* Moench DQ88368	*vulgaris* AJ871487 T. Eriksson 821 (SBT) AM116870	*vulgaris* AJ416467	–	–	–	–	*vulgaris* U06804	*vulgaris* AJ416463
Fragaria	*ananassa* Rozier X15590	*vesca* L. AJ871486	*vesca* AJ511771	*vesca* Potter 970209-01 (DAV) AF196891	–	*vesca* AF288102	*vesca* DQ851521	*ananassa* U06805	*vesca* AJ512232
Geum	–	*urbanum* L. AJ534193 Smedmark 3 (S) AM116871	*urbanum* AJ302337	–	–	–	*macrophyllum* Willd. DQ851522	*chiloense* Balb. L01921	*urbanum* AJ297323
Gillenia	*trifoliata* (L.) Moench DQ88369	*trifoliata* (L.) Moench AF500431 - AF500432 DQ874890 - DQ874891	*stipulata* (Muhl. ex Willd.) Baill. DQ811763	*stipulata* UC Bot. Gard. 92.0438 AF196913	*stipulata* UC Bot. Gard. 92.0438 DQ851205	*stipulata* AF288103	*trifoliata* DQ851523	*stipulata* DQ250747 Robertson s.n. (ILLS)	*stipulata* AF348554

Table 2. (Continued)

Hagenia	–	–	*abyssinica* (Bruce) J. F. Gmel. U90800	–	–	–	–	–	*abyssinica* AY634727
Heteromeles	–	*arbutifolia* Roemer AF500433 - AF500435	*arbutifolia* U16193	*arbutifolia* Gao s.n. (DAV) AF196894	*arbutifolia* Gao s.n. (DAV) DQ851207	*arbutifolia* DQ860464	*arbutifolia* DQ851524	–	*arbutifolia* DQ863236
Holodiscus	*discolor* (Pursh) Maxim. DQ88370	–	*microphyllus* Rydb. UCD Arbor. A89.0417 DQ88361	*microphyllus* UCD Arbor. A89.0417 AF196895	*microphyllus* UCD Arbor. A89.0417 DQ851208	*discolor* AF288105	*discolor* Potter 970517-07 (DAV) DQ851525	*discolor* U06807	*discolor* AF348546
Kageneckia	–	*oblonga* Ruiz & Pav. AF285980 - AF285982 DQ874892 - DQ874894	*angustifolia* D. Don DQ811764	*oblonga* UC Bot. Gard. 88.0176 AF196898	*oblonga* UC Bot. Gard. 88.0176 DQ851209	*angustifolia* DQ860447	*angustifolia* DQ851526	*angustifolia* U06808	*oblonga* AF348547
Kelseya	–	–	–	–	–	*uniflora* (S. Wats.) Rydb. D. Barton 2218 (DAV) DQ851226	–	–	*uniflora* D. Barton 2218 DQ851232
Kerria	*japonica* (L.) DC. AF132890	*japonica* DQ904404	*japonica* Potter s.n. (DAV) DQ88360	–	–	–	*japonica* DQ851527	*japonica* DQ250749 Morton Arb. Acc. 466-78	–
Leucosidea	–	–	*sericea* Eckl. & Zeyh. AF183547, AF183524	–	–	–	–	–	*sericea* AJ512222
Lindleya	–	*mespiloides* Kunth AF500436 - AF500438 DQ874895	*mespiloides* DQ811764	–	–	*mespiloides* DQ860448	*mespiloides* DQ851528	*mespiloides* U06810	*mespiloides* DQ863220
Luetkea	–	–	*pectinata* (Pursh) Kunze Morgan 2284 (WWB) DQ851235	–	–	*pectinata* Potter 011020-02 (DAV) DQ851227	–	*pectinata* Morgan 2284 (WWB) DQ250750	*pectinata* Morgan 2284 (WWB) DQ851233
Lyonothamnus	*floribundus* Gray DQ88371	*floribundus* AF500439	*floribundus* AY555315	*floribundus* Gao s.n. (DAV) AF196903	*floribundus* Gao s.n. (DAV) DQ851210	*floribundus* AF288107	*floribundus* Gao s.n. (DAV) DQ851529	*floribundus* U06811	*floribundus* AF348548
Maddenia	–	–	*hypoleuca* Koehne AF179549, AF179550	–	–	*hypoleuca* Lee & Wen 5005 (CS) DQ851228	–	–	*hypoleuca* AY864827
Malacomeles	–	*denticulata* (Kunth) Engler AF500440 - AF500441	*denticulata* U16194	–	–	*denticulata* DQ860465	*denticulata* DQ851520	–	*denticulata* DQ863237
Malus	–	*sargentii* Rehder AF285983 - AF285985 AF500442	*domestica* Borkh. U16195	–	–	*sargentii* DQ860466	*domestica* DQ851531	–	*sargentii* DQ863238

Margyricarpus	–	–	*cristatus* Britton. AJ512777	–	–	–	*pinnatus* (Lam.) Kuntze DQ851532	–	*cristatus* AJ512782
Mespilus	–	*germanica* L. AF500443 - AF500446	*germanica* U16196	–	–	*germanica* DQ860467	*germanica* DQ851533	–	*germanica* DQ863239
Neillia	(*Stephanandra incisa* (Thunb.) Zabel) DQ88381	(*Stephanandra incisa*) AF500469	*thyrsiflora* D. Don AF487148	–	*thyrsiflora* DXP 170 DQ851211	*thyrsiflora* AF288108	*sinensis* Oliv. DXP 103 DQ851534	*sinensis* U06813	*thyrsiflora* AF487229
Neviusia	*alabamensis* A. Gray DQ88372	–	–	*alabamensis* UC Bot. Gard. 93.0973 AF196906	–	*alabamensis* AF288109	*alabamensis* DQ851535	*alabamensis* U06815	*alabamensis* AF348550
Oemleria	–	*cerasiformis* (Torr. & Gray ex Hook. & Arn.) Landon AF285986	*cerasiformis* AF318715	–	*cerasiformis* Bortiri 129 (DAV) DQ851212	*cerasiformis* AF288110	*cerasiformis* Bortiri 129 (DAV) DQ851536	*cerasiformis* U06816	*cerasiformis* AF348551
Osteomeles	–	*anthyllidifolia* L. AF285987 - AF285988 DQ874888 - DQ874889	*schwerinae* Schneider U16197	–	–	*schwerinae* DQ860468	*schwerinae* DQ851537	–	*schwerinae* DQ863240
Peraphyllum	–	*ramosissimum* Nutt. AF500447 - AF500449 DQ874903	*ramosissimum* U16198	–	–	*ramosissimum* DQ860469	*ramosissimum* DQ851538	–	*ramosissimum* DQ863241
Petrophyton	–	–	*caespitosum* (Nutt.) Rydb. Potter 020906-02 (DAV) DQ851236	–	–	*caespitosum* Potter 020906-02 (DAV) DQ851229	–	–	*caespitosum* Potter 020906-02 (DAV) DQ851234
Photinia	*fraseri* Dress U42800	*villosa* (Thunb,) DC. AF500450 - AF500452	–	*serrulata* Lindl. UC Davis Potter 970911-01 AF196907	–	*villosa* DQ860470	*villosa* DQ851539	*fraseri* L11200	*villosa* DQ863242
Physocarpus	*opulifolius* (L.) Maxim. DQ88373	*opulifolius* AF285989	*opulifolius* AY555326	*capitatus* (Pursh) Kuntze Potter 970702-01 (DAV) AF196908	*capitatus* Potter 970702-01 (DAV) DQ851213	*capitatus* AF288112	*opulifolius* DQ851540	*malvaceus* (Greene) Kuntze U06817	*capitatus* AF348553
Polylepis	–	–	*tarapacana* Phil. AJ512773	–	–	–	–	–	*tarapacana* AJ512778
Potaninia	–	–	*mongolica* Maxim Norlindh and Ahti 10384 (S) AM286742	–	–	–	–	–	*mongolica* Norlindh and Ahti 10384 (S) AM286742
Potentilla	*indica* (Andrews) T. Wolf DQ88374	–	*reptans* L. U90784	*anserina* L. Potter 970309-02 (DAV) AF196916	–	*anserina* AF288113	–	–	*reptans* AJ512241

Table 2. (Continued)

Poteridium	–	–	*annuum* (Nutt. ex Hook.) Spach AY635032	–	–	–	–	–	*annuum* AY634766
Poterium	–	–	*sanguisorba* L. AY634772	–	–	–	sp. DQ851541	–	*sanguisorba* AY635038
Prinsepia	*uniflora* Batal. DQ88375	*sinensis* (Oliv.) Oliv. ex Bean AF285990	*sinensis* AF318751	*sinensis* Harvard Univ. AF196919	*sinensis* Harvard Univ. DQ851215	*sinensis* AF288114	*sinensis* DQ851542	*uniflora* U06819	*sinensis* AF348558
Prunus	*virginiana* L. DQ88377	*virginiana* AF285991 AF500453	*laurocerasus* L. AF318724	–	–	*laurocerasus* AF288116	*carolinana* (P. Mill.) Ait. DQ851544	*laurocerasus* U06809	*laurocerasus* AF348559
Prunus	*dulcis* (Mill.) D. A. Webb DQ88376		*persica* (L.) Batsch AF318741	*dulcis* 'Padre' Bortiri 68 (DAV) AF196923	*dulcis* 'Padre' Bortiri 68 (DAV) DQ851216	*dulcis* AF288115	*dulcis* Bortiri 68 (DAV) DQ851543	*persica* AF206813	*persica* AF348560
Pseudocydonia	–	*sinensis* (Thouin) Schneider AF500454 DQ874911	*sinensis* U16201	–	–	*sinensis* DQ860471	*sinensis* DQ851545	–	*sinensis* DQ863243
Purshia	*tridentata* DC. DQ88378	*tridentata* DQ904405	*tridentata* Potter 970831-02 (DAV) DQ88357	*tridentata* Potter 970831-02 (DAV) AF196927	–	*tridentata* AF288119	*tridentata* Potter 970831-02 (DAV) DQ851546	*tridentata* U06821	*tridentata* AF348562
Pygeum	–	–	–	–	–	*topengii* Merr. Wen 5813 (F) DQ851230	–	–	–
Pyracantha	–	*coccinea* Roemer AF500455-AF500456	*coccinea* DQ811772	–	–	*coccinea* DQ860472	*coccinea* DQ851547	–	*coccinea* DQ863244
Pyrus	*communis* L. AF195622	*calleryana* Decne. AF500457-AF500459 DQ874900 DQ875905	*calleryana* U16202	–	*caucasica* Fed. DQ851218	*calleryana* DQ860473	*communis* DQ851548	–	*calleryana* DQ863245
Rhamnus	*cathartica* L. - AJ235979	*cathartica* AF285992	*cathartica* AY626436	*californica* (Eschsch.) A. Gray UCD Arb. A93.0177 AF196933	*californica* UCD Arb. A93.0177 DQ851196	*californica* AF288121	*cathartica* DQ851549	*cathartica* L13189	*californica* AF348565
Rhaphiolepis	–	*indica* (L.) Lindley AF500460-AF500462	*indica* U16203	–	–	*indica* DQ860474	*indica* DQ851550	–	*indica* DQ863246
Rhodotypos	*scandens* (Thunb.) Mak. DQ88379	*scandens* DQ904406	*scandens* UC Bot. Gard. 86.0616 AY177141	*scandens* UC Bot. Gard. 86.0616 AF196936	*scandens* UC Bot. Gard. 86.0616 DQ851219	*scandens* AF288122	–	*scandens* U06823	*scandens* AF348566
Rosa	*hybrida* L. X66773	*multiflora* Thunb. AF285993	*majalis* Herrm. U90801	–	–	*californica* Cham. & Schlecht. AF288123	*blanda* Ait. DQ851551	*woodsii* Lindl. U06824	*majalis* AJ512229

Rubus	*idaeus* L. DQ88380	*odoratus* L. AF285994	*chamaemorus* L. U90803	–	–	*ursinus* Cham. & Schlecht. AF288124	*idaeus* DQ851552	*idaeus* U06825	*chamaemorus* AJ416464
Sanguisorba	–	–	*officinalis* L. AY635041	–	–	–	–	*officinalis* AY395560	officinalis AJ416465
Sibbaldia	–	–	*procumbens* L. U90820, U90821	–	–	–	–	–	*procumbens* AJ512235
Sibbaldianthe	–	–	*bifurca* (L.) Kurtto & T. Eriksson U90786	–	–	–	–	–	*bifurca* AJ512224
Sieversia	–	*pentapetala* (L.) Greene AJ871484 T. Eriksson 749 (SBT) AM116872	*pentapetala* AJ302359	–	–	–	–	–	*pentapetala* AJ297345
Sorbaria	–	*sorbifolia* (L.) A. Br. AF500463 - AF500464, DQ904407	*sorbifolia* AF318758	*sorbifolia* UC Bot. Gard. 83.0529 AF196947	–	*sorbifolia* AF288125	*sorbifolia* DQ851553	*arborea* Schneid. U06826	*sorbifolia* AF348569
Sorbus	–	*americana* Marsh. AF500465 - AF500468 DQ874905	*aucuparia* L. U16204	–	*californica* Greene Oh s.n. (DAV) DQ851220	*californica* AF288126	*americana* DQ851554	*scopulina* Greene U06827	*americana* DQ863247
Spenceria	–	–	–	–	–	–	sp. DQ851555	–	*ramalana* Trimen DQ88383
Spiraea	X*bumalda* Burvenich. U42801	*trilobata* L. DQ904408	*densiflora* Nutt. Potter 970619-02 (DAV) DQ88362	*densiflora* Potter 970619-02 (DAV) AF196949	*densiflora* Potter 970619-02 (DAV) DQ851222	*densiflora* AF288127	*cantoniensis* Lour. UCD Arb. DQ851556	X*vanhouttei* (Briot) Zabel L11206	*densiflora* AF348571
Spiraeanthus	–	–	–	–	–	–	*schrenckianus* (Fisch. & Mey.) Maxim. DQ851557	–	–
Stranvaesia	–	*davidiana* Decne. AF500470 – AF500473	–	–	–	*davidiana* DQ860476	*davidiana* DQ851558	–	*davidiana* DQ863248
Torminalis	–	*clusii* (Roemer) Robertson & Phipps AF500474 – AF500475	*clusii* DQ811773	–	–	*clusii* DQ860477	*clusii* DQ851559	–	*clusii* DQ863249
Vauquelinia	*californica* (Torr.) Sarg. DQ88382	*californica* AF285995 - AF285998	*californica* AY555316	*californica* UCD Arbor. A77.0200 AF196954	*californica* UCD Arbor. A77.0200 DQ851223	*californica* AF288129	*californica* DQ851560	*corymbosa* Correa U06829	*californica* AF348573

(PPO9: TCCACAACTCCTGGCTCTT and PPO10: TTCTCGTTGTAAAACAAGAA) were also designed. PCR amplification and sequencing followed the methods described above for *pgip*.

*trn*L-F: Amplification and sequencing used the c-f primer pair of Taberlet et al. (1991). Methods are described in Eriksson et al. (2003). Sequence fragments were proof-read and assembled using the Staden Package (Staden 1996).

gbssi: New sequences were obtained using methods described by Evans et al. (2000) or Smedmark et al. (2003)

Data Analyses. Sequences of all regions were aligned manually, in some cases using Se-Al (Rambaut 1996), and/or ClustalX (Thompson et al. 1997). For *pgip* and *ppo*, nucleotides were aligned to amino acid alignments using DAMBE (Xia and Xie 2001). Introns (*gbssi*1, *gbssi*2, and some *pgip* sequences) and ambiguously aligned regions were excluded from all subsequent analyses.

Each of the ten loci was analyzed separately for all taxa for which data were available. A combined data matrix comprising all ten loci and 91 taxa, representing 88 genera of Rosaceae, with *Ceanothus* L. and *Rhamnus* L. (Rhamnaceae) included as outgroups (Table 2), was assembled by combining sequences of members of the same genus, and, when possible, the same species from all of the different regions. We sought to include one species from most currently recognized genera of Rosaceae. Based on the results of previous phylogenetic studies (Lee and Wen 2001; Bortiri et al. 2001, 2002; Shaw and Small 2004), two composite taxa were used to represent the diversity within the large genus *Prunus*; one corresponding to the *Amygdalus*/*Armeniaca*/*Prunus* (peach-almond/apricot/plum) clade and the other to the *Cerasus*/*Laurocerasus*/*Padus* (cherry/laurel-cherry) clade. In cases where recent phylogenetic evidence strongly supports inclusion of one genus within another, we included only one species to represent both. For example, we did not include separate representatives for *Stephanandra* and *Neillia* because recent evidence showed that the former genus is nested within the latter and the two have now been merged (Oh 2006). In two other cases, a genus was represented even though it had already been combined with another, because no molecular phylogenetic study in support has yet been published. One such case pertains to *Pygeum*, which was transferred to *Prunus* by Kalkman (1965), the other to *Cowania*, which was transferred to *Purshia* by Henrickson (1986).

In Rosoideae, several genera were lumped into *Potentilla* (*Duchesnea*, *Horkelia*, and *Ivesia*) based on previous analyses (Eriksson et al. 1998, 2003), and into *Geum* (*Novosieversia*, *Erythrocoma*, *Oncostylus*, *Acomastylis*, and *Taihangia*; see Smedmark, 2006). Material was not available for *Stellariopsis*, *Comarella*, and *Purpusia*, but according to preliminary study of morphology they are expected to be included in *Potentilla*. *Fragaria* is not combined with *Potentilla*, as suggested by Mabberley (2002), because it would make *Potentilla* polyphyletic. Generic delimitations in Sanguisorbeae follow Kerr (2004).

For three genera of Spiraeeae (Table 1), material was not available, but Potter et al. (2007) support inclusion of both *Sibiraea* and *Xerospiraea* in the tribe. No data at all were available for the monotypic Korean genus *Pentactina*.

For cloned sequences (*gbssi*1, *gbssi*2, *pgip*, and *ppo*), one clone per taxon was selected randomly. Missing data were coded as necessary for particular locus-genus combinations. Sequence alignments are available from the corresponding author.

In addition to simultaneous analyses of all ten loci, analyses of various partitions of the total data set were also conducted (Table 3). Because of some questionable results of analyses of *pgip* and *ppo* (see Results), analyses were run excluding those two loci. The four chloroplast loci were analyzed in combination, as were the six nuclear loci, and the four nuclear loci other than *pgip* and *ppo*. In the last two cases, five taxa (*Coleogyne*, *Cowania*, *Kelseya*, *Pygeum*, *Spenceria*, *and Spiraeanthus*), for which there were no data from any nuclear locus, were omitted.

Phylogenetic analysis of the data employing maximum parsimony was implemented in the UNIX version of PAUP* 4.0 b10 (Swofford 2002) using heuristic searches and 1,000 replicates of random taxon addition with TBR branch-swapping, MulTrees in effect, and maxtrees allowed to increase automatically as necessary for most data sets. In order to expedite the search on the ITS data set, a maximum of 100 trees were saved per replicate. In four cases (*mat*K, *ndh*F, *trn*L-*trn*F, and the combined chloroplast loci), because of the large number of most parsimonious trees ($>600,000$) recovered on the first replicate in preliminary analyses, an alternative search strategy was ultimately used to maximize the chances that we had indeed recovered the shortest possible trees: 20,000 replicates of random addition sequence, saving a single tree per replicate. All positions were weighted equally; gaps were treated as missing values. Branch support was assessed using 10,000 parsimony bootstrap replicates, each with a single random addition sequence replicate and TBR branch-swapping saving a single tree per replicate.

Bayesian analyses, using models of sequence evolution for each data partition selected in MrAIC (Nylander 2005), were implemented in MrBayes 3.1.1 (Huelsenbeck and Ronquist 2001). For each data set and combination of data sets, double analyses were run with four chains for 1,000,000 generations, sampling every 100 generations. Burn-in was set to 100,000 generations, except for the *trn*L-*trn*F data set where burn-in was set to 200,000 generations. The sampled trees from both analyses were pooled and majority-rule consensus trees were constructed from the remaining 18,000 (16,000 in the case of *trn*L-*trn*F) trees to estimate Bayesian clade credibility values.

Non-molecular character states were scored according to our own observations and published reports (Table 4). A primary objective of this project was to use our phylogenies to study the evolution of fruits, for which we needed detailed information on mature fruit characteristics. Sufficiently detailed data for some taxa (i.e. Pyrinae) were available from the literature, but for many genera more detailed information was necessary. This information was produced by obtaining mature fruiting material, dissecting the fruits, and recording detailed observations on their structure. MacClade 4.06 (Maddison and Maddison 2003) was used to map non-molecular character states and geographic distributions by continent (Hutchinson 1964) onto one of the most parsimonious trees obtained from the phylogenetic analyses of molecular data.

Taxonomy. Our primary criterion for formal taxonomic recognition of groups was strong support by the data. In order to be given formal recognition, a clade had to meet *all* of the following specific criteria: 1) Congruence among data sets: Monophyly of the group must not be strongly (95% or greater parsimony bootstrap support and/or 95% or greater Bayesian clade credibility) contradicted by any analysis of a single data partition or any combination of partitions. 2) Robustness: Monophyly of the group must be supported with at least 85% parsimony bootstrap support and 95% Bayesian clade credibility in the combined analysis of all data sets. 3) Consistency with previous classifications: As much as possible within the constraints of recognizing only putatively monophyletic groups, we sought to make our classification maximally consistent with previous classifications, in terms of the numbers and circumscriptions of subfamilies and tribes.

Names were selected for subfamilies, tribes, and subtribes following the rules of the International Code of Botanical Nomenclature (ICBN, Greuter et al. 2000). Authorship, priority, and valid publication of names were determined by examining original publications and by consulting several sources (Kalkman 2004, Reveal 2004, Pankhurst 2005, International Plant Names Index 2006).

Results

The total number of characters, number of parsimony informative characters, number of taxa, number and statistics of most parsimonious trees recovered, and model of sequence evolution selected for each of our data partitions are presented in Table 3, while the significant clades supported by various analyses are summarized in Table 5. Clades are here designated using the taxonomic names listed in column 1 of Table 1.

Phylogenetic analyses of the nuclear genes *pgip* and *ppo* both produced results (not shown) that were inconsistent in some ways with the majority of the other data and with each other and that are therefore considered anomalous. In the case of *pgip*, parsimony analyses placed Rosoideae sister to Osmaronieae with moderate (71% parsimony bootstrap) support and Spiraeeae sister to that clade with weak (34% parsimony bootstrap) support; neither of these relationships was supported by Bayesian analysis. The *ppo* data provided strong (75% parsimony bootstrap, 100% Bayesian clade credibility) support for a sister relationship between Osmaronieae and Spiraeeae, in conflict with the chloroplast data,

Table 3. Characteristics of molecular data sets included in this study

Region	Number of taxa (alone / combined)	Aligned length	Number Included	Number Informative	Model	Number MPT	Length	CI (*)	RI
*mat*K	64 / 64	1576	1558	346	GTR-G	> 600,000	1170	.6855 (.5671)	.8172
*ndh*F	66 / 64	1106	1106	298	GTR-G	> 600,000	1165	.5717 (.4893)	.7796
*rbc*L	50 / 43	1547	1436	207	GTR-I-G	8	731	.5267 (.4401)	.7136
*trn*L-*trn*F	85 / 85	1452	1295	333	GTR-G	> 600,000	1296	.6451 (.5486)	.8600
18S	28 / 28	1654	1654	63	GTR-I-G	1134	238	.6807 (.5097)	.6530
*gbssi*1	46 / 46	941	941	277	GTR-I-G	462	1220	.5336 (.4422)	.6711
*gbssi*2	43 / 43	941	941	282	GTR-G	18,456	1155	.5688 (.4813)	.6862
ITS	81 / 80	793	702	368	GTR-G	1600	2624	.3605 (.3151)	.5994
pgip	31 / 29	841	841	370	HKY-G	2	1616	.5291 (.4697)	.6069
ppo	28 / 25	1416	1416	614	GTR-G	4	2358	.5356 (.4959)	.6861
All partitions	91	12,267	11,890	3084	GTR-G	1214	13631	.5246 (.4446)	.6872
All but *pgip*, *ppo*	91	10,010	9633	2131	GTR-G	226	9682	.5225 (.4302)	.7112
chloroplast only	91	5681	5395	1141	GTR-G	> 600,000	4312	.6143 (.5100)	.8008
nuclear only	85	6586	6495	1943	GTR-G	15,389	9226	.4880 (.4225)	.6180
nuclear except *pgip*, *ppo*	85	4329	4238	990	HKY-I-G	1824	5304	.4554 (.3782)	.6220

* excluding autapomorphies

Table 4. Non-molecular characters of particular phylogenetic interest in the Rosaceae. Characters 1-12 are mapped in Fig. 2; character 13 is mapped in Fig. 3, and character 14 is mapped in Fig. 4

Character	States	Description	References
1. Ovary connation	0	absent	Hutchinson 1964; Robertson, Phipps, and Rohrer 1991
	1	present	
2. Style connation	0	absent	Hutchinson 1964; Robertson, Phipps, and Rohrer 1991; Evans and Dickinson 1999a, 1999b; Evans and Dickinson 2005
	1	present	
3. Enlarged receptacle	0	present	Hutchinson 1964
	1	absent	
4. Pistil number	0	one	Hutchinson 1964; Robertson, Phipps, and Rohrer 1991; Rohrer, Robertson, and Phipps 1994
	1	one-five	
	2	> five	
5. Ovary-hypanthium adnation	0	no	Hutchinson 1964; Robertson, Phipps, and Rohrer 1991; Rohrer, Robertson, and Phipps 1994
	1	yes	
6. Nitrogen fixation	0	present	Benson and Silvester 1993
	1	absent	
7. Sorbitol production	0	absent	Wallaart 1980
	1	trace < 1.0% of dry leaves	
	2	present > 1.0% of dry leaves	

Table 4. (Continued)

Character	States	Description	References
8. Base chromosome number	0	7	Roitman et al. 1974, Missouri Botanical Garden 2005
	1	8	
	2	9	
	3	12	
	4	15	
	5	17	
9. Leaf morphology	0	compound	Hutchinson 1964
	1	simple	
10 Stipules	0	present	Hutchinson 1964
	1	absent	
	2	deciduous	
11. *Gymnosporangium* host	0	no	Savile 1979; Farr 1989; Farr et al. 2005
	1	yes	
12. *Phragmidium* host	0	no	Savile 1979; Farr 1989; Farr et al. 2005
	1	yes	
13. Ovule number/locule and position with respect to each other	0	one	Hutchinson 1964; Sterling 1964, 1965a, 1965b, 1965c, 1966; Robertson, Phipps, and Rohrer 1991; Evans 1999; Evans and Dickinson 1999b; Evans and Dickinson 2005
	1	two/collateral	
	2	two/superposed	
	3	> two/clustered	
	4	> 2/files	
14. Fruit type	0	pome	Hutchinson 1969; Spjut 1994
	1	polypyrenous drupe	
	2	drupe	
	3	drupetum	
	4	achene	
	5	achenetum	
	6	follicetum	
	7	coccetum	
	8	nucculanium	

which strongly supported monophyly of Kerriodae, the clade comprised of Osmaronieae and Kerrieae. Including *pgip* and *ppo* in the combined data set favored, with strong support (93% parsimony bootstrap and 100% Bayesian clade credibility) the resolution obtained with *ppo* alone (Table 5). Similarly, the sister relationship between *Lyonothamnus* and the rest of Spiraeoideae, strongly supported by the chloroplast data, was lost when *pgip* and *ppo* were included in the combined analysis. These anomalous results led us to question the reliability of the *pgip* and *ppo* results, at least with respect to the relationships mentioned. We therefore constructed trees based on a data matrix consisting of all sequences except *pgip* and *ppo*. The strict consensus tree resulting from parsimony analysis of all sequences except *pgip* and *ppo* is shown in Figure 1. The distributions of states of selected non-molecular characters of interest (Table 4) were mapped onto one of the most parsimonious trees from this analysis (Figs. 2–4), revealing varying degrees of homoplasy in non-molecular characters with respect to hypotheses of phylogenetic relationship based on molecular data.

The results of our phylogenetic analyses, combined with our criteria for taxonomic recognition of clades (see Materials and methods), have led us to propose the classification presented in Table 1 and described in further detail below (see Discussion). We recognize three subfamilies: Rosoideae, Dryadoideae, and Spiraeoideae. Within Rosoideae, we recognize one supertribe, three tribes, and three subtribes, and within Spiraeoideae we recognize two supertribes, seven tribes, and one subtribe.

Discussion

Phylogenetic resolution. Phylogenetic analyses of combined sequence data from nuclear and chloroplast loci (Table 3) provided strong support for all of the infrafamilial taxa recognized here (Table 1). All of these groups were also supported by the chloroplast data alone, but not all were supported by the nuclear loci alone (Table 5). Furthermore, the signal in the *pgip* and *ppo* data differed enough from the chloroplast loci with respect to the resolution of relationships among tribes within Spiraeoideae so as to result in conflicting topologies of the trees produced from the data set including all loci and the one including all loci minus *pgip* and *ppo*. In particular, whereas in trees resulting from both the combined cpDNA data set and the combined chloroplast and nuclear data set excluding *pgip* and *ppo*, *Lyonothamnus* was sister to all other Spiraeoideae and monophyly of Kerriodae (Osmaronieae plus Kerrieae) was strongly supported, neither of those relationships was supported in the combined data set including all loci.

In the case of both *pgip* and *ppo*, we do not have a definitive explanation for the anomalous results but we cannot rule out the possibility of incorrect orthology assessment (suggested by some strong conflicts with the other data sets) and/or long branch attraction (suggested by some differences between results of parsimony and Bayesian analyses). Because we had concerns about the validity of some of the relationships resolved by *pgip* and *ppo* data, we chose to use the topology supported by the data set excluding *pgip* and *ppo* for optimization of non-molecular characters. On the other hand, inclusion of the *pgip* and *ppo* data did not violate any of the criteria for taxonomic recognition of any group to which we have given such recognition. It is also noteworthy that the nuclear loci alone provided generally weak and/or conflicting resolutions among the tribes in Spiraeeae (Table 5). This could be taken as suggestive of hybridization among the ancestors of these lineages, but it is difficult to draw any definitive conclusions because the taxon sampling was different for each locus.

The combined data set of eight regions and 88 genera of Rosaceae is missing almost 40% of the data. The average number of gene regions for which sequences are available (Table 2) is 4.9 (± 2.2). To determine whether

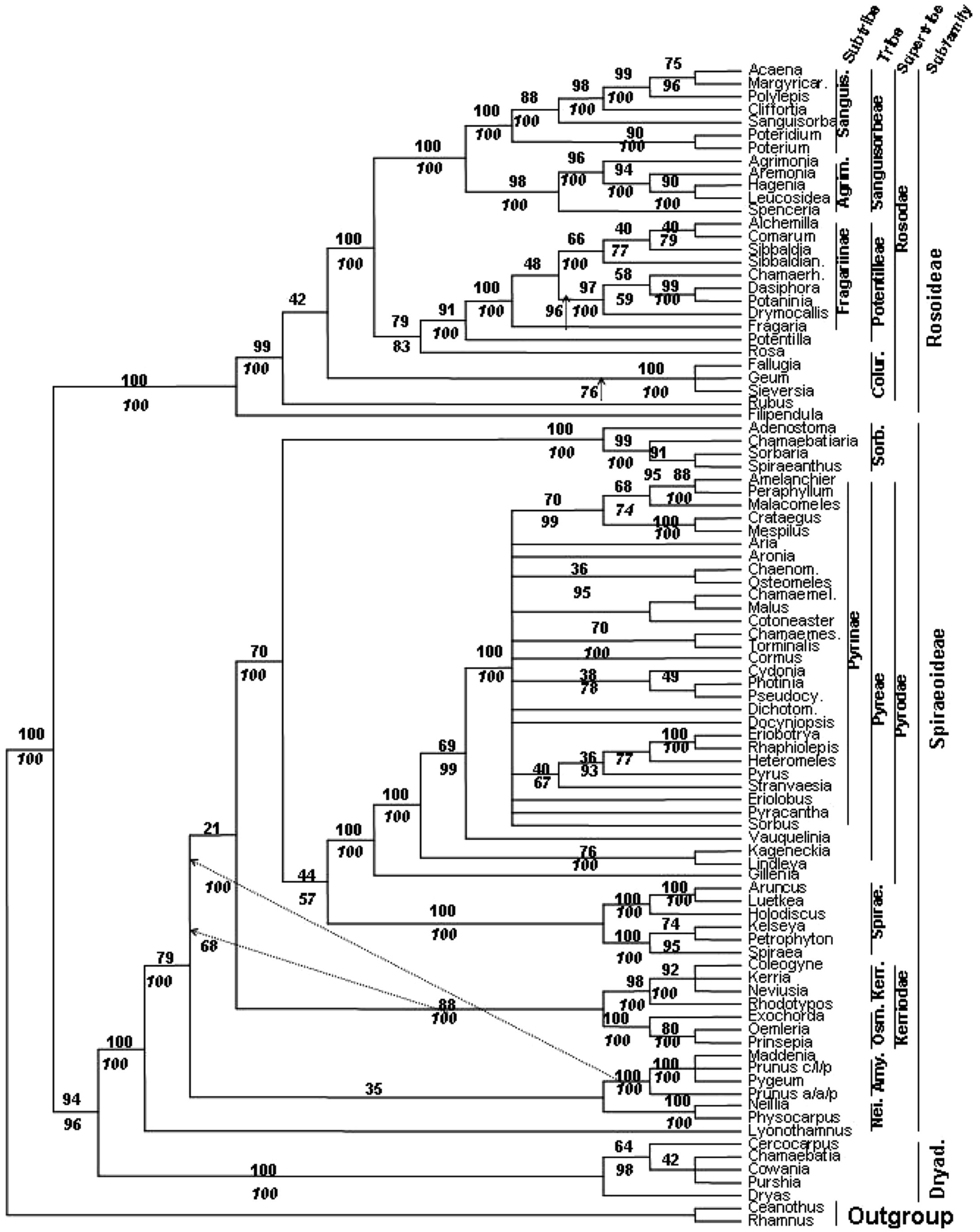

Fig. 1. Strict consensus of 226 most parsimonious trees (l = 9,682, ci = 0.5225 (0.4302 excluding autapomorphies), ri = 0.7112) from phylogenetic analysis of all data partitions except *pgip* and *ppo*. Bootstrap (above branches) and Bayesian clade credibility (below branches, in italics) support values are indicated. Arrows are used to indicate groups that were supported by the Bayesian analysis but were not recovered in the strict consensus tree. (In the Bayesian tree, the branching order within Spiraeoideae was: *Lyonothamnus*; Neillieae; (the branch leading to the remainder of the subfamily supported with 68% clade credibility), Kerriodae; (the branch leading to the remainder of the subfamily supported with 100% clade credibility), Amygdaleae; the rest of the subfamily)

Character	States		
1. Ovary connation	0 = absent	1= present	
2. Style connation	0 = absent	1= present	
3. Enlarged receptacle	0 = present	1 = absent	
4. Pistil number	0 = one	1 = one-five	2 = >five
5 Ovary-hypanthium adnation	0 = no	1 = yes	
6. Nitrogen fixation	0 = present	1 = absent	
7. Sorbitol production	0 = absent	1= trace 2 = present	
8. Base chromosome number	0 = 7 2 = 9 4 =15	1 = 8 3 = 12 5 = 17	
9. Leaf morphology	0 = compound	1 = simple	
10. Leaf stipules	0 = present	1 = absent 2 = deciduous	
11. Gymnosporangium host	0 = no	1 = yes	
12. Phragmidium host	0 = no	1 = yes	

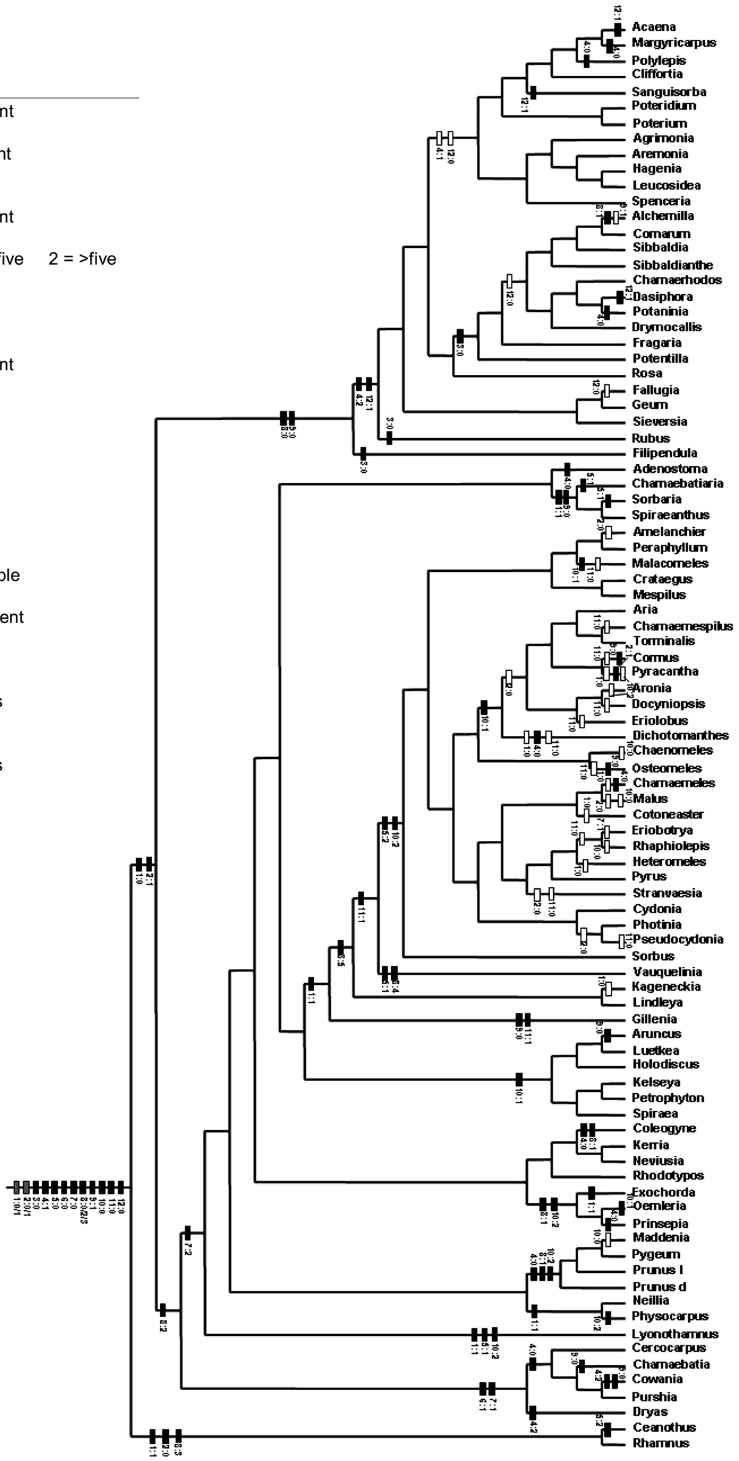

Fig. 2. Hypothesis for character evolution of 12 morphological, chemical, and fungal host associations. Character states were mapped onto one of the 226 most parsimonious trees. Characters and states correspond to those listed 1–12 in Table 4**.** Character state changes along branches are labelled as follows: black boxes are apomorphies (syn-, aut-); white boxes are reversals; gray boxes are unresolved. Character states were optimized in MacClade using DELTRAN

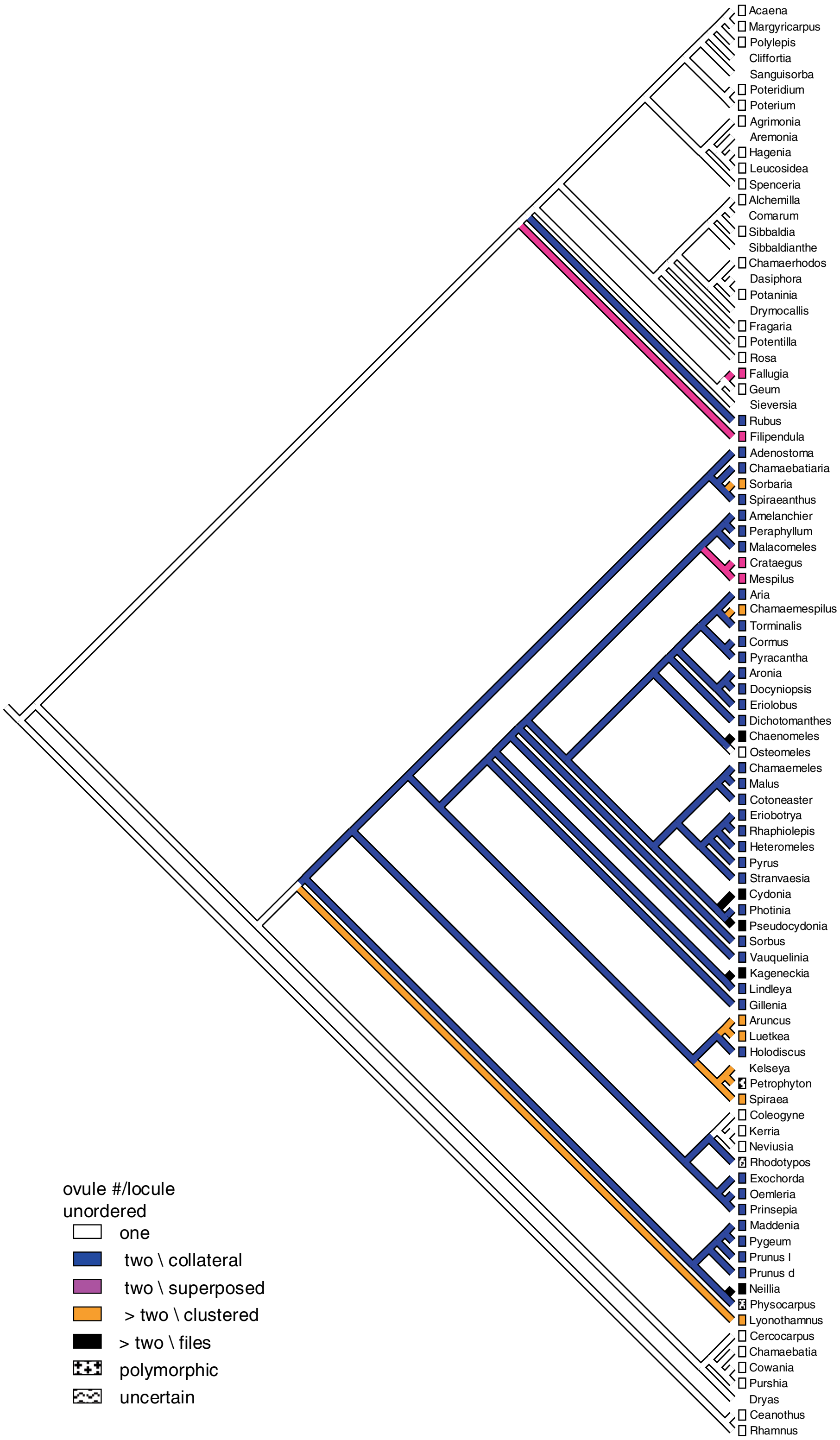

Fig. 3. Hypothesis for evolution of ovule number and position with ovary locule (Character 13 in Table 4). Character states were mapped onto one of 226 most parsimonious trees (identical to the one used in Fig. 2). Character states were optimized in MacClade using DELTRAN

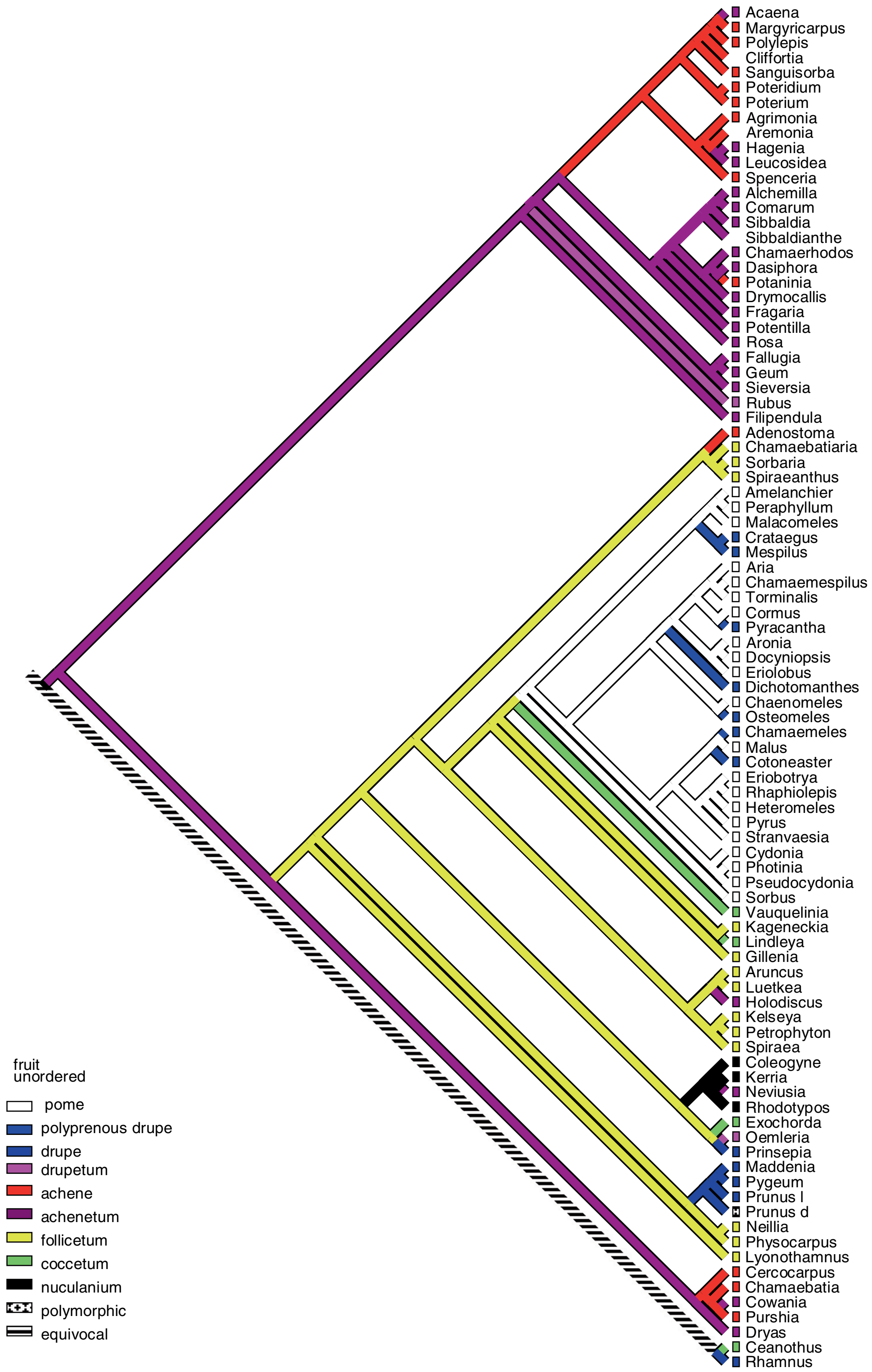

Fig. 4. Hypothesis for evolution of Rosaceae fruit type (Character 14 in Table 4). Character states were mapped onto one of 226 most parsimonious trees (identical to the one used in Fig. 2). Character states follow Spjut (1994) and were optimized in MacClade using DELTRAN

Table 5. Support values (parsimony bootstrap / Bayesian clade credibility) for various clades by various data partitions. Only clades with at least 85% bootstrap or 95% Bayesian clade credibility support from at least one data partition are included. The composition of the clades varies among the different analyses due to differences in taxon sampling among the different partitions (see Tables 2 and 3). The designation "na" means the relevant taxa were not included to test support for the clade in question; "–" means the clade was not compatible with the 50% majority-rule bootstrap tree or that it was supported with less than 50% Bayesian clade credibility; "*" means that it was compatible with the 50% majority-rule bootstrap tree but was not recovered in the strict consensus tree (parsimony) for the data set in question; "**" means that it was not compatible with the 50% majority-rule bootstrap tree but it was recovered in the strict consensus tree (parsimony) for the data set in question. In the case of *gbssi*2, no outgroups were included in the analysis; trees were therefore rooted between Rosoideae and the rest of the family, consistent with the results from most of the other data sets

Clade	18S	*gbssi*1	*gbssi*2	ITS	*pgip*	ppo	matk	*ndh*F	*rbc*L	*trn*L-*trn*F	All nuclear	Nuclear except pgip, ppo	Chloro-plast only	All Loci	All except pgip and ppo
1. Rosoideae	73 / 97	96 / 100	100 / 100	73 / 100	100 / 100	100 / 100	100 / 100	100 / 100	100 / 100	90 / 98	90	89 / 100	99 / 100	100 / 100	100 / 100
2. Dryadoideae	86 / 100	na	100 / 100	100 / 100	95 / 100	100 / 100	94 / 100	99 / 100	99 / 100	100 / 100	100	100 / 100	100 / 100	100 / 100	100 / 100
3. Spiraeoideae	– / –	49* / 90	68 / 96	44 / 79	– / –	73 / 100	94 / 100	51 / 100	30 / 52	64 / 98	94	87 / 100	99 / 100	100 / 100	100 / 100
4. Colurieae	na	98 / 100	97 / 100	88 / 100	na	na	na	50* / 100	98 / 100	100 / 98	100	100 / 100	99 / 100	100 / 100	100 / 100
5. Potentilleae	– / –	na	na	– / –	na	na	93 / 100	75 / 100	99 / 100	90 / 100	–	– / –	99 / 100	99 / 100	91 / 100
6. Sanguisorbeae	na	na	na	23* / –	na	na	na	99 / 100	99 / 100	100 / 100	28*	32* / –	100 / 100	100 / 100	100 / 100
6a. Sanguisorbinae	na	na	na	32* / 94	na	na	na	75 / 73	na	100 / 100	42	35* / 98	100 / 100	100 / 100	100 / 100
6b. Agrimoniinae	na	na	na	99 / 100	na	na	na	na	na	98 / 100	99	99 / 100	98 / 100	98 / 100	98 / 100
7. Amygdaleae	92 / 100	na	na	97 / 100	100 / 100	100 / 100	100 / 100	100 / 100	98 / 100	100 / 100	98	99 / 100	100 / 100	100 / 100	100 / 100
8. Osmaronieae	100 / 100	38* / 58	100 / 100	100 / 100	100 / 100	100 / 100	100 / 100	100 / 100	99 / 100	100 / 100	100	100 / 100	100 / 100	100 / 100	100 / 100
9. Kerrieae	– / –	42* / 100	na	– / –	56 * / 97	na	99 / 100	100 / 100	83 / 100	77 / 99	54	– / 82	100 / 100	100 / 100	98 / 100
10. Neillieae	57* / 100	99 / 99	na	100 / 100	100 / 100	100 / 100	100 / 100	100 / 100	76 / 100	100 / 100	100	100 / 100	100 / 100	100 / 100	100 / 100
11. Pyrodae	– / –	96 / 100	100 / 100	77 / 100	100 / 100	100 / 100	100 / 100	100 / 100	100 / 100	100 / 98	99	99 / 85	100 / 100	100 / 100	100 / 100
11a. Pyreae	– / –	74 / 100	99 / 100	– / –	79 / 99	99 / 100	65 / 85	76 / 74	76 / 66	92 / 98	95	92 / 85	100 / 100	100 / 100	100 / 100
11b. Pyrinae	57* / 69	84 / 100	83 / 100	48 / 94	100 / 100	100 / 100	70 / 100	24* / 92	55 / 89	93 / 98	95	97 / 89	99 / 100	100 / 100	100 / 100
12. Sorbarieae	70* / 98	100 / 100	100 / 100	100 / 100	100 / 100	100 / 100	100 / 100	100 / 100	95 / 100	100 / 100	100	99 / 100	100 / 100	100 / 100	100 / 100
13. Spiraeeae	93 / 100	na	96 / 100	95 / 100	100 / 100	100 / 100	100 / 100	100 / 100	97 / 100	100 / 100	100	90 / 99	100 / 100	100 / 100	100 / 100
1 plus 2	– / –	– / –	na (root)	– / –	– / –	– / –	– / 78	– / –	– / 64	– / –	–	– / –	– /–	– / –	– / –
2 plus 3	44* / 79	38* / 51	na (root)	52 / –	– / –	71 / 99	46 / –	68 / 99	35 / –	64 / 98	88	67 / 84	89 / 90	98 / 100	94 / 96
1 plus 3	– / –	– / –	na (root)	– / –	55 / –	– / –	– / –	– / –	– / –	– / –	–	– / –	– / –	– / –	– / –
Kerriodae (8 plus 9)	– / –	– / –	na	7 / –	– / –	– / –	57 / 100	39* / 80	– / –	49 / 74	–	31* / 83	94 / 100	– / –	88 / 100
1 except *Filipendula*	– / –	56* / –	96 / 100	– / –	na	na	na	na	86 / 70	100 / 98	–	46 / 91	100 / 100	99 / 100	99 / 100
1 except *Filipendula* and *Rubus*	– / –	79 / 100	97 / 100	– / –	na	na	na	– / –	– / –	79 / –	–	– / –	– / –	50 / –	42 / –
1 except *Filipendula*, *Rubus*, and 4	na	na	na	– / –	na	na	na	36 / 73	90 / 100	98 / 100	51*	53 / 100	99 / 100	100 / 100	100 / 100
Rosa plus 5	– / –	92 / 100	na	– / –	na	na	99 / 100	47 / 85	82 / 87	– / –	22	– / –	80 / 97	71 / 87.5	79 / 83

3 except *Lyonothamnus*	– / –	na	– / –	– / –	– / –	– / –	85 / 100	33 / 99	– / –	82 / 98	–	– / –	98 / 100	– / –	79 / 100
3 except 7	– / –	– / –	– / –	– / –	– / –	– / 99	– / –	– / –	– / –	– / –	–	–/–	– / –	– / –	– / –
3 except 10	– / –	12* / 74	na	16 / 86	– / –	36 / –	– / –	– / –	– / –	– / –	41	36 / 100	– / –	42 / 64 and < 50	– / –
7, 11, 12, and 13	– / –	– / –	– / –	– / 93	– / –	– / –	37 / 99	– / –	– / –	– **/ 98	–	– / –	65 / 100	– / –	– / 100
11, 12 , and 13	– / –	– / –	– / –	54 / 88	– / –	– / –	– / –	– / –	– / –	– / 92	–	42 / 84	– / 87	– / –	70 / 100
Lyonothamnus plus 8, 9, 12, and 13	– / –	na	na	– / –	– / –	72 / 100	– / –	– / –	– / –	– / –	53	– / –	– / –	46 / 99.5	– / –
Lyonothamnus plus 8, 12, and 13	– / –	na	– / –	– / –	– / –	52 / 100	– / –	– / –	– / –	– / –	–	– / –	– /	– / –	– / –
Lyonothamnus plus 9 and 12	– / –	na	– / –	– / –	– / –	– / –	– / –	– / –	– / –	– / –	38	– / –	– / –	34 / 99.5	– / –
8 plus 13	– / –	na	– / –	– / –	– / –	75 / 100	– / –	– / –	– / –	– / –	77	– / –	– / –	93 / 100	– / –
9 plus 12	– / –	26* / 95	na	– / –	– / –	– / –	– / –	– / –	– / –	– / –	35	– / –	– / –	– / –	– / –
9 plus 10	– / –	– / –	na	– / –	30* / 95	– / –	– / –	– / –	– / –	– / –	–	– / –	– / –	– / –	– / –

our results in analysis of the data set of 88 genera were affected by missing data, we assembled a data set for all 10 regions with two exemplars each from Rosoideae, Dryadoideae, Osmaronieae, Kerrieae, Neillieae, *Prunus*, Pyreae, Sorbarieae, and Spiraeeae as well as *Lyonothamnus*, Results of parsimony analyses of this exemplar data set (not shown) agree with the analyses of the 88-genus data set in strongly supporting these major groups as well as the Spiraeoideae as we circumscribe it and in uncertainty about relationships among the three subfamilies and among most tribes of Spiraeoideae. Hence we are confident that missing data do not affect our conclusions, consistent with the simulation study by Wiens (2003).

Our results agree with all previous phylogenetic analyses of Rosaceae in providing little resolution along the backbone of the Rosaceae phylogenetic tree. Resolution is especially poor among tribes of Spiraeoideae, where various groupings received generally weak or moderate support, depending on the data set and method of analysis (Table 5). Most of the resolution present in Fig. 1 is provided by our chloroplast loci, but it is important to note that the chloroplast loci were also more thoroughly sampled than the nuclear loci. Most of our data support a sister relationship between Rosoideae and the other two subfamilies, but there is also some support for a sister relationship between Rosoideae and Dryadoideae (Table 5). Both rapid evolutionary radiation of lineages and reticulations among the ancestors of those lineages are possible explanations for these patterns. These processes have been implicated in the evolution of the Pyreae (Campbell et al. 2007).

Patterns of character evolution. With the caveat that relationships among Rosales and other members of the nitrogen-fixing clade of eurosids I remain poorly resolved (Angiosperm Phylogeny Group 2003), our parsimony reconstruction analyses support the following ancestral states within Rosaceae: shrubs with alternate simple leaves, sorbitol absent, stipules present, stamens numerous (> 10), pistils 1–5, hypanthium free from ovaries, ovaries separate, styles free, one ovule per locule, and fruit an achenetum or follicetum. The ancestral base chromosome number for the family is either 7 or 9. Each of the following character states evolved independently two or more times within the family (Fig. 2): trees and herbs, compound leaves, loss of stipules (several times in Spiraeoideae), base chromosome number $x = 8$ (once in Rosoideae and several times in Spiraeoideae), ovary connation (several clades in Spiraeoideae, especially Pyreae), style connation (several derivations within Pyreae), enlarged receptacle (several derivations within Rosoideae), and basal adnation of the ovary and hypanthium (several derivations within Spiraeoideae). Each of several conditions of ovule number and position also evolved multiple times (Fig. 3). According to our results, each of the following character states may have evolved only once in the family: hypanthium adnate to the ovary for more than half of its length (Pyrinae; one reversal), base chromosome number $x = 17$ (15) (Pyreae), and presence of sorbitol as a primary transport carbohydrate (Dryadoideae plus Spiraeoideae).

The traditional view of fruit evolution within Rosaceae, as exemplified by the four-subfamily classification (e.g. Schulze-Menz 1964) was quite simple, with the derived fruit types (pome, drupe, achene) originating once each from ancestral follicles. In contrast, our results agree with other molecular phylogenetic studies (Morgan et al. 1994, Potter et al. 2002) in suggesting that the evolution of fruit types in the family has been much more complex (Fig. 4). Some clades are relatively homogeneous. The Rosoideae and Dryadoideae all have indehiscent one-seeded fruits, and the Pyrinae all have the mature gynoecium enclosed by a fleshy hypanthium (although there is considerable variation in what the receptacle and hypanthium develop into in Rosoideae and in what the carpels develop into in Pyrinae). The remaining clades are all heterogeneous with respect to fruit type. For example, two of the clades that have follicle/follicetum fruits also contain a genus bearing achene/achenetum fruits: *Adenostoma* in Sorbarieae and *Holodiscus* in Spiraeeae. Three of the four clades (Amygdaleae, Kerrieae, Osmaronieae, and Pyrinae) containing genera in which pericarps are drupaceous (having a stony endocarp) also contain genera that have non-drupaceous pericarps: *Neviusia* in Kerrieae, *Exochorda* in Osmaronieae, and several genera in Pyrinae.

The overall picture of the evolution of fruits in Rosaceae is not one in which specific combinations of characteristics have consistently evolved together to yield distinct fruit types (i.e., follicles, achenes, pomes, drupes, etc.), but one in which several different fruit characteristics have evolved more or less independently, producing genera and groups of genera that exhibit different combinations of these characteristics. One of several examples is provided by fruits in which the pericarp is drupaceous. As mentioned above, genera with drupaceous pericarps are found in four clades: Pyrinae, Kerrieae, Osmaronieae, and Amygdaleae. However, the drupaceous pericarps in each of these clades are accompanied by various characteristics that make them different from one another. For example, the drupaceous pericarps in Pyrinae (polyprenous drupes of *Crataegus* and others) are accompanied by fleshy hypanthia that enclose the mature gynoecium, which do not occur in the other three drupaceous clades. Another example is seen in the drupaceous fruits of Kerrieae, which do not have the fleshy mesocarps that are found in all three of the other drupaceous clades.

Several ecological associations exhibit taxonomic distributions that appear to correlate with phylogenetic relationships within Rosaceae (Fig. 2). Symbiotic nitrogen fixation, via associations with actinomycetes of the genus *Frankia*, has been observed only in Dryadoideae, in which members of all four genera have been reported to form nodules. This association is also found in some members of seven other families of orders Rosales, Cucurbitales, and Fagales. These three orders, along with Fabales, form a subclade, sometimes designated the nitrogen-fixing clade (APG 2003), within the eurosid I clade. Association with rust fungi of the genus *Gymnosporangium* appears to be restricted to Pyrodae, while association with *Phragmidium* rusts has been reported only from members of Rosoideae. In both cases, however, sampling has been quite limited.

The clades resolved within Rosaceae by our analyses provide numerous examples of intriguing biogeographic patterns, including the eastern Asia – eastern and western North America pattern exemplified by Neillieae (Oh and Potter 2005) and Kerrieae, a central and eastern Asia – western North America pattern in Sorbarieae and Osmaronieae, and potentially complex patterns involving multiple continents in groups such as Rosoideae, Spiraeeae, Pyrodae, and Amygdaleae. With the exception of *Dryas*, which has a circumpolar distribution, taxa of Dryadoideae are restricted to western North America, and throughout much of that region the nitrogen-fixing *Frankia* strains with which they form symbioses show remarkably little genetic diversity (Vanden Heuvel et al. 2004). The phylogenetic trees generated by our analyses suggest a North American origin for the entire family, each of the three subfamilies, and Pyrodae. However, a series of detailed studies with thorough sampling of species within each tribe, aimed at achieving considerably increased phylogenetic resolution, will be required to tease apart all of the complexities of geographic patterns across the family.

Classification. A new, phylogenetically based classification for Rosaceae is proposed based on the results of our analyses (Table 1), following the criteria listed above (see Materials and Methods).

Some clades received strong support in the combined analysis but did not meet all three of the criteria outlined above; such clades have therefore not been given taxonomic recognition here. Thus, no name is given to either the clade comprising Dryadoideae plus Spiraeoideae or the clade including all members of Spiraeoideae except *Lyonothamnus*.

We have chosen to recognize three clades at the supertribal level: Rosodae, comprising all Rosoideae except *Filipendula*; Kerriodae, comprising Kerrieae plus Osmaronieae, and Pyrodae, comprising Pyreae (all with $x = 15$ or 17) plus *Gillenia*. The inclusion of supertribes allows us to incorporate greater phylogenetic resolution while maintaining a ranked classification than would be possible without addition of this rank. In order to minimize the number of names of different ranks that refer to the same groups, we chose not to name supergeneric taxa that would include, based on current phylogenetic evidence, only one genus. An exception was made for *Prunus*, which we place in tribe Amygdaleae due to the large size and diversity of the genus and the limited sampling to date of species sometimes classified in *Maddenia* and *Pygeum*. In Rosoideae, *Filipendula* is included in the subfamily but not in any tribe, *Rosa* and *Rubus* are both included in Rosodae but not in any tribe, and *Potentilla* is included in Potentilleae but not in any subtribe, although the remaining genera are placed in Fragariinae. In Spiraeoideae, *Lyonothamnus* is included in the subfamily but is not in any tribe, *Gillenia* is included in Pyrodae but not in any tribe, and *Kageneckia, Lindleya*, and *Vauquelinia* are included in Pyreae but not in any subtribe, although the remaining genera are classified in Pyrinae. Our subtribe Pyrinae corresponds to the long-recognized subfamily Maloideae (Schulze-Menz 1964) in which the fruit type is generally a pome. *Pyrus* was selected as the type genus for its subtribe and tribe in accordance with the ICBN (Greuter et al. 2000, Art. 11.5). The two names available for the subtribe are Mespilinae and Pyrinae, both published by Du Mortier (1827) and therefore of equal priority. Since, to our knowledge, no one has previously published a choice between these two names (Greuter et al. 2000, Art. 11.5), we here select the latter. The tribal name Maleae (Schulze-Menz 1964) was nomenclaturally superfluous when published since Schulze-Menz listed Sorbeae (Koehne 1890) as a synonym; Pyreae (Baillon 1869) has priority over both Sorbeae and Crataegeae

(Koehne 1890). The name Pomeae A. Gray (1842) is invalid because it is a descriptive name, not based on the name of an included genus (Greuter et al. 2000, Arts. 18.1, 19.3). The three supertribal names, Rosodae, Kerriodae, and Pyrodae, are published here for the first time.

Taxonomic treatment: infrafamilial classification of Rosaceae. In the following descriptions, potential synapomorphies are indicated in bold font. Based on the current results of our analyses, we complement the traditional classification with phylogenetic definitions of the hypothesized clades. More detailed discussion of the classification of Pyrinae is presented by Campbell et al. (2007).

Family Rosaceae Juss., Gen. Pl. 334 (1789), nom. cons.: the clade comprising Rosoideae (cf. below), Dryadoideae (cf. below), and Spiraeoideae (cf. below).

Included taxa: Rosoideae, Dryadoideae, and Spiraeoideae.

Distinctive non-molecular features: Herbs, shrubs, and trees. Cyanogenic glycosides often present. Sorbitol often present as a transport carbohydrate. Leaves generally alternate, simple to variously divided or compound. Stipules present except where noted. Flowers generally perfect. Sepals and petals generally 5, **stamens** (0–3)5-**many**, pistils (0)1 – many. Hypanthium present; free from to fully adnate to the ovary(ies). Ovaries separate or connate. Styles free except in some Pyreae. Fruit an achene, achenetum (multiple achenes from a single flower), follicetum (multiple follicles from a single flower), coccetum (multiple carpels from a single flower, separating at maturity and each dehiscing along two sutures, sometimes described as a capsule), drupe, drupetum (multiple drupelets from a single flower), nuculanium (similar to drupe or drupetum except that the mesocarp is not fleshy), polyprenous drupe, or pome (descriptive fruit terminology from Spjut 1994). Base chromosome number $x = 7$, 8, 9, 15, or 17.

Subfamily Rosoideae (Juss.) Arn., Encycl. Brit., ed. 7, 5: 107 (1832): the most inclusive clade containing *Rosa* (as typified by *Rosa cinnamomea* L.), but not Dryadoideae (cf. below) nor Spiraeoideae (cf. below).

Included taxa: *Filipendula*, Rosodae.

Distinctive non-molecular features: Perennial or, rarely, annual herbs, shrubs, or, rarely, trees. Cyanogenic glycosides absent. Sorbitol absent. Leaves alternate and usually **compound**. Stipules present. Pistils 1-many. Receptacle sometimes enlarged. Hypanthium free from ovaries. Ovaries separate. Fruits indehiscent. **Base chromosome number $x = 7$** (8).

Filipendula Adans.

Distinctive non-molecular features: Receptacle enlarged. Pistils 1–5. Fruit an achenetum.

Rosodae T. Eriksson, Smedmark, and M. S. Kerr, supertribus nova Supertribus analysibus phylogeneticis ordinum ADN genorum chloroplastorum et nucleorum recognoscitur et valde sustinetur.

Supertribe Rosodae T. Eriksson, Smedmark, and M. S. Kerr: the most inclusive clade containing *Rosa* (as typified by *Rosa cinnamomea* L.), but not *Filipendula* (as typified by *Filipendula vulgaris* Moench).

Included taxa: *Rosa*, *Rubus*, Sanguisorbeae, Potentilleae, Colurieae.

The supertribe Rosodae exhibits the range of character states found in Rosoideae, but excludes *Filipendula*.

Rosa L. (including *Hulthemia* Dumort.)

Distinctive non-molecular features: Shrubs. Pistils numerous. Hypanthium concave, urn-shaped. Fruit an achenetum.

Rubus L. (including *Dalibarda* L.)

Distinctive non-molecular features: Mostly shrubs. Receptacle enlarged. Pistils numerous. **Fruit a drupetum.**

Tribe Sanguisorbeae DC., Prodr. 2: 588 (1825): Sanguisorbeae and the enclosed subtribes Sanguisorbinae and Agrimoniinae conform to definitions by Eriksson et al. (2003).

Included taxa: Sanguisorbinae, Agrimoniinae

Distinctive non-molecular features: Pistils 1–5. Fruit an achene or achenetum.

Subtribe Agrimoniinae J. Presl, Wsobecny Rostl. 1: 502 (1846). Included taxa: *Agrimonia* L., *Aremonia* Neck. ex Nestl., *Hagenia* J. F.

Gmel., *Leucosidea* Eckl. & Zeyh., *Spenceria* Trimen

Distinctive non-molecular features: Herbs, shrubs (*Leucosidea*), or trees (*Hagenia*).

Subtribe Sanguisorbinae Torr. & A. Gray, Fl. N. Amer. 1: 428 (1840). Included taxa: *Cliffortia* L., *Acaena* L., *Margyricarpus* Ruiz & Pav. (including *Tetraglochin* Poepp.), *Polylepis* Ruiz & Pav., *Poterium* L. (including *Bencomia* Webb & Berthel., *Marcetella* Svent., *Dendriopoterium* Svent., and *Sarcopoterium* Spach), *Poteridium* Spach, *Sanguisorba* L.

Distinctive non-molecular features: Herbs, shrubs (*Margyricarpus*, some *Cliffortia*, *Polylepis*, and *Poterium*), or trees (some *Polylepis*).

Tribe Potentilleae Sweet, Brit. Fl. Gard. 2: 124 (1825): Potentilleae and the enclosed *Potentilla* and subtribe Fragariinae conform to definitions by Eriksson et al. (2003).

Included taxa: *Potentilla*, Fragariinae.

Distinctive non-molecular features: Herbs or shrubs (*Dasiphora*, *Potaninia*, and some *Comarum*). Leaves often simple in *Alchemilla*. **Enlarged receptacle common** (absent in *Alchemilla* and *Potaninia*). Pistils with lateral to basal styles. Pistils generally numerous (solitary in *Potaninia* and some *Alchemilla*). Fruit an achenetum or achene.

Base chromosome number $x = 7$ (8 in *Alchemilla*).

Potentilla L. (including *Argentina* Lam., *Comarella* Rydb., *Duchesnea* Sm., *Horkelia* Cham. & Schltdl., *Horkeliella* (Rydb.) Rydb., *Ivesia* Torr. & A. Gray, *Purpusia* Brandegee, and *Stellariopsis* (Baill.) Rydb.)

Distinctive non-molecular features: none known.

Subtribe Fragariinae Torr. & A. Gray, Fl. N. Amer. 1: 435 (1840). Included taxa: *Alchemilla* L. (including *Aphanes* L., *Lachemilla* (Focke) Lagerh., and *Zygalchemilla* Rydb.), *Chamaerhodos* Bunge, *Comarum* L. (including *Farinopsis* Chrtek & Soják), *Dasiphora* Raf. (= *Pentaphylloides* Duhamel), *Drymocallis* Fourr., *Fragaria* L., *Potaninia* Maxim., *Sibbaldianthe* Juz. (including *Schistophyllidium* (Juz. ex Fed.) Ikonn.), *Sibbaldia* L., *Sibbaldiopsis* Rydb.

Distinctive non-molecular features: none known.

Tribe Colurieae Rydb., N. Amer. Fl. 22: 397 (1913): Colurieae conforms to the definition in Smedmark and Eriksson (2002).

Included taxa: *Geum* L. (including *Acomastylis* Greene, *Coluria* R. Br., *Novosieversia* F. Bolle, *Oncostylus* (Schltdl.) F. Bolle, *Orthurus* Juz., *Taihangia* T. T. Yü & C. L. Li, and *Waldstenia* Willd.), *Fallugia* Endl., *Sieversia* Willd.

Distinctive non-molecular features: Pistils usually numerous. **Receptacle often enlarged**. Fruit an achenetum or achene.

Subfamilies Dryadoideae plus Spiraeoideae Base chromosome number $x = 8$ or higher. Sorbitol present.

Subfamily Dryadoideae Juel, Kongl. Svenska Vetensk. Akad. Handl. n.s. 58: 55 (1918): the most inclusive clade containing *Dryas* (as typified by *Dryas octopetala* L.), but not Rosoideae (cf. above) nor Spiraeoideae (cf. below).

Included taxa: *Cercocarpus* H. B. & K., *Chamaebatia* Benth., *Dryas* L., *Purshia* DC. (including *Cowania* D. Don)

Distinctive non-molecular features: Shrublets, shrubs, or small trees. **Symbiotic nitrogen fixation present.** Cyanogenic glycosides present. Sorbitol present in trace amounts. Leaves compound in *Chamaebatia*, simple in the other genera. Stipules present. Hypanthium free from ovary. Pistils 1 (*Cercocarpus*, *Chamaebatia*, *Purshia*) or 4-many (*Cowania, Dryas*). Fruit an achene or achenetum. Base chromosome number $x = 9$.

Subfamily Spiraeoideae C. Agardh, Cl. Pl. 20 (1825): the most inclusive clade containing *Spiraea* (as typified by *Spiraea salicifolia* L.), but not Rosoideae (cf. above) nor Dryadoideae (cf. above).

Included taxa: *Lyonothamnus*, Amygdaleae, Neillieae, Sorbarieae, Spiraeeae, Kerriodae, Pyrodae

Distinctive non-molecular features: Mostly shrubs and trees. Sorbitol present in significant amounts. Cyanogenic glycosides generally present. Leaves generally simple and alternate. Stipules usually present. Pistils 1–5. Hypanthium generally free from ovary(ies). Ovaries generally separate. Fruit a **follicetum**, achene, achenetum, coccetum, drupe, drupetum, nuculanium, polyprenous drupe, or pome. Base chromosome number $x = 8, 9, 15$, or 17.

Lyonothamnus A. Gray

Distinctive non-molecular features: Cyanogenic glycosides absent. **Leaves opposite**, entire or deeply divided. **Stipules deciduous. Hypanthium adnate to base of ovaries. Ovaries connate**; hypanthium adnate to base. Fruit a follicetum. Base chromosome number $x = 9$.

Tribe Amygdaleae Juss., Gen. Pl. 340 (1789): the most inclusive clade containing *Prunus amygdalus* (L.) Batsch (= *Amygdalus communis* L.) but not Osmaronieae (cf. below), Kerrieae (cf. below), Neillieae (cf. below), Sorbarieae (cf. below), Spiraeeae (cf. below), or Pyrodae (cf. below).

Included taxa: *Prunus* L. (including *Amygdalus* L., *Armeniaca* Juss., *Cerasus* Mill., *Laurocerasus* Tourn. ex Duhamel, *Maddenia* Hook. F. & Thomson, *Padus* Mill., and *Pygeum* Gaertn.)

Distinctive non-molecular features: Stipules deciduous. **Pistil solitary. Fruit a drupe. Base chromosome number $x = 8$**.

Tribe Neillieae Maxim., Trudy Imp. S.-Peterburgsk. Bot. Sada 6: 216 (1879): the most inclusive clade containing *Neillia* (as typified by *Neillia thyrsiflora* D. Don) but not Amygdaleae (cf. above), Osmaronieae (cf. below), Kerrieae (cf. below), Sorbarieae (cf. below), Spiraeeae (cf. below), or Pyrodae (cf. below).

Included taxa: *Neillia* D. Don (including *Stephanandra* Siebold & Zucc.,), *Physocarpus* (Cambess.) Raf.

Distinctive non-molecular features: Cyanogenic glycosides absent in *Physocarpus*, no data for the other genera. Stipules deciduous in *Physocarpus*. **Ovaries connate.** Fruit a follicetum. Base chromosome number $x = 9$.

Tribe Sorbarieae Rydb., N. Amer. Fl. 22: 256 (1908): the most inclusive clade containing *Sorbaria* (as typified by *Sorbaria sorbifolia* (L.) A. Braun) but not Amygdaleae (cf. above), Osmaronieae (cf. below), Kerrieae (cf. below), Neillieae (cf. above), Spiraeeae (cf. below), or Pyrodae (cf. below).

Included taxa: *Adenostoma* Hook. & Arn., *Chamaebatiaria* Maxim., *Sorbaria* A. Braun, *Spiraeanthus* Maxim.

Distinctive non-molecular features: Leaves fascicled or alternate and simple in *Adenostoma*, alternate and compound in the remaining genera. **Ovaries connate** (pistil solitary in *Adenostoma*); hypanthium adnate to base in *Chamaebatiaria* and *Sorbaria*. Fruit an achene (*Adenostoma*) or follicetum. Base chromosome number $x = 9$.

Tribe Spiraeeae DC., Prodr. 2: 541 (1825): the most inclusive clade containing *Spiraea* (as typified by *Spiraea salicifolia* L.), but not Amygdaleae (cf. above), Osmaronieae (cf. below), Kerrieae (cf. below), Neillieae (cf. above), Sorbarieae (cf. above), or Pyrodae (cf. below).

Included taxa: *Aruncus* Adans., *Holodiscus* Maxim., *Kelseya* Rydb., *Luetkea* Bong. (= *Eriogynia* Hook.), *Petrophyton* Rydb., *Sibiraea* Maxim., *Spiraea* L., *Xerospiraea* J. Henrickson. *Pentactina* Nakai may belong here but has not been included in phylogenetic analyses to date.

Distinctive non-molecular features: Herbs (*Aruncus*) or shrubs, sometimes forming rosettes.

Stipules absent. Fruit a follicetum or achenetum (*Holodiscus*). Base chromosome number $x = 9$.

Kerriodae D. Potter, S. H. Oh, and K. R. Robertson, supertribus nova Supertribus analysibus phylogeneticis ordinum ADN genorum chloroplastorum et nucleorum recognoscitur et valde sustinetur.

Supertribe Kerriodae D. Potter, S. H. Oh, and K. R. Robertson: the clade comprising Kerrieae (cf. below) and Osmaronieae (cf. below) if they are sister-groups.

Included taxa: Kerrieae and Osmaronieae.

Tribe Osmaronieae Rydb., N. Amer. Fl. 22: 482 (1918): the most inclusive clade containing *Oemleria* (as typified by *Oemleria cerasiformis* (Hook. & Arn.) J. W.Landon) but not Amygdaleae (cf. above), Kerrieae (cf. below), Neillieae (cf. above), Sorbarieae (cf. above), Spiraeeae (cf. above), or Pyrodae (cf. below).

Included taxa: *Exochorda* Lindl., *Oemleria* Rchb., *Prinsepia* Royle (including *Plagiospermum* Oliv.)

Distinctive non-molecular features: **Stipules absent in *Oemleria*, deciduous in the other genera.** Ovaries connate in *Exochorda*.

Fruit a coccetum (*Exochorda*), drupetum (*Oemleria*), or drupe (*Prinsepia*). **Base chromosome number $x = 8$.**

Tribe Kerrieae Focke, Nat. Pflanzenfam. ed. 1, 3: 27 (1888): the most inclusive clade containing *Kerria* (as typified by *Kerria japonica* (L.) DC.) but not Amygdaleae (cf. above), Osmaronieae (cf. above), Neillieae (cf. above), Sorbarieae (cf. above), Spiraeeae (cf. above), or Pyrodae (cf. below).

Included taxa: *Coleogyne* Torr., *Kerria* DC., *Neviusia* A. Gray, *Rhodotypos* Siebold & Zucc.

Distinctive non-molecular features: Leaves opposite in *Coleogyne* and *Rhodotypos*. Pistil solitary in *Coleogyne*. **Fruit a nuculanium** (achenetum in *Neviusia*). Base chromosome number $x = 9$ (8 in *Coleogyne*).

Pyrodae C. S. Campbell, R. C. Evans, D. R. Morgan, and T. A. Dickinson, supertribus nova Supertribus analysibus phylogeneticis ordinum ADN genorum chloroplastorum et nucleorum recognoscitur et valde sustinetur.

Supertribe Pyrodae C. S. Campbell, R. C. Evans, D. R. Morgan, and T. A. Dickinson: the most inclusive clade containing *Pyrus* (as typified by *Pyrus communis* L.) but not Amygdaleae (cf. above), Osmaronieae (cf. above), Kerrieae (cf. above), Neillieae (cf. above), Sorbarieae (cf. above), or Spiraeeae (cf. above).

Included taxa: *Gillenia* Moench, Pyreae.

Distinctive non-molecular features: Perennial herbs (*Gillenia*), trees, or shrubs. Leaves compound in *Gillenia*, *Cormus*, *Osteomeles*, and some *Sorbus*. **Hosts to *Phragmidium* and *Gymnosporangium* rusts;** ovaries generally connate (separate or single ovaries in *Kageneckia* and some members of Pyrinae (*Chamaemeles*, *Cotoneaster*, *Dichotomanthes*, *Heteromeles*, and *Pyracantha*)); ovules basal, paired, collateral, with **funicular obturators.**

Tribe Pyreae Baill., Hist. Pl. 1: 442, 475 (1869): the most inclusive clade containing *Pyrus* (as typified by *Pyrus communis* L.) but not *Gillenia* (as typified by *Gillenia trifoliata* (L.) Moench) or Spiraeeae (cf. above)

Included taxa: *Kageneckia* Ruiz & Pav., *Lindleya* H. B. & K., *Vauquelinia* Correa ex Humb. & Bonpl., Pyrinae.

Distinctive non-molecular features: **base chromosome number $x = 17$** ($x = 15$ in *Vauquelinia*)**.**

Subtribe Pyrinae Dumort. Fl. Belg.: 92 (1827): the most inclusive clade containing *Pyrus* (as typified by *Pyrus communis* L.) but not *Gillenia* (as typified by *Gillenia trifoliata* (L.) Moench), *Vauquelinia* (as typified by *Vauquelinia corymbosa* Bonpl.), *Kageneckia* (as typified by *Kageneckia oblonga* Ruiz & Pav.) or *Lindleya* (as typified by *Lindleya mespiloides* Kunth).

Included taxa: *Amelanchier* Medik., *Aria* J. Jacq., *Aronia* Pers., *Chaenomeles* Lindl., *Chamaemeles* Lindl., *Chamaemespilus* Medik., *Cormus* Spach, *Cotoneaster* Medik., *Crataegus* L., *Cydonia* Mill., *Dichotomanthes* Kurz, *Docynia* Decne., *Docyniopsis* (C. K. Schneid.) Koidz., *Eriobotrya* Lindl., *Eriolobus* Roemer, *Hesperomeles* Lindl., *Heteromeles* M. Roem., *Malacomeles* G. N. Jones, *Malus* Mill., *Mespilus* L., *Osteomeles* Lindl., *Peraphyllum* Nutt. ex Torr. & Gray, *Photinia* Lindl., *Pseudocydonia* C. K. Schneid., *Pyracantha* M. Roem., *Pyrus* L., *Rhaphiolepis* Lindl., *Sorbus* L., *Stranvaesia* Lindl., *Torminalis* Medik. This subtribe corresponds to the long-recognized subfamily Maloideae.

Distinctive non-molecular features: **Hypanthium adnate to more than half of the ovary** (except *Dichotomanthes*). **Stamens 20. Fruit a pome** or polypyrenous drupe. **Prismatic crystals in axial parenchyma**. Cyanogenic glycosides absent in some genera (additional sampling needed).

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References

Angiosperm Phylogeny Group (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.

Baillon H. (1869) Histoire des plantes, vol. 1. Librairie de L. Hachette, Paris.

Benson D. R., Silvester W. B. (1993) Biology of *Frankia* strains, actinomycete symbionts of actinorhizal plants. Microbiol. Rev. 57: 293–319.

Bortiri E., Oh S., Gao F., Potter D. (2002) The phylogenetic utility of nucleotide sequences of sorbitol 6-phosphate dehydrogenase in *Prunus* (Rosaceae). Amer. J. Bot. 89: 1697–1708.

Bortiri E., Oh S., Jiang J., Baggett S., Granger A., Weeks C., Buckingham M., Potter D., Parfitt D. (2001) Phylogeny and systematics of *Prunus* (Rosaceae) as determined by sequence analysis of ITS and the chloroplast *trn*L-*trn*F spacer DNA. Syst. Bot. 26: 797–807.

Boss P. K., Gardner R. C., Janssen B. J., Ross S. P. (1995) An apple polyphenol oxidase cDNA is up-regulated in wounded tissues. Pl. Molec. Biol. 27: 429–433.

Campbell C. S., Donoghue M. J., Baldwin B. G., Wojciechowski M. F. (1995) Phylogenetic relationships in Maloideae (Rosaceae): evidence from sequences of the internal transcribed spacers of nuclear ribosomal DNA and its congruence with morphology. Amer. J. Bot. 27: 903–918.

Campbell C. S., Evans R. C., Morgan, D. R., Dickinson T. A., Arsenault M. P. (2007) Phylogeny of subtribe Pyrinae (formerly the Maloideae, Rosaceae): limited resolution of a complex evolutionary history. Pl. Syst. Evol. 266: 119–145.

Chevalier T., de Rigal D., Mbeguie-AMbeguie D., Gauillard F., Richard-Forget F., Fils-Lycaon B. R. (1999) Molecular cloning and characterization of apricot fruit polyphenol oxidase. Pl. Physiol. (Lancaster) 119: 1261–1270.

Chevreau E., Laurens F. (1987) The pattern of inheritance in apple (*Malus* × *domestica* Borkh.): further results from leaf isozyme analysis. Theor. Appl. Genet. 75: 90–95

Chevreau E., Lespinasse Y., Gallet M. (1985) Inheritance of pollen enzymes and polyploid origin of apple (*Malus* × *domestica* Borkh.). Theor. Appl. Genet. 71: 268–277.

Cronquist A. (1981) An integrated system of classification of flowering plants. Columbia University Press, New York.

Cuatrecasas J. (1970) Flora Neotropica Monograph No. 2, Brunelliaceae. Hafner, Darien, Connecticut.

Du Mortier B.-C. (1827) Florula belgica: operis majoris prodromus. J. Casterman, Tournay.

Eriksson T., Donoghue M. J., Hibbs, M. S. (1998) Phylogenetic analysis of *Potentilla* using DNA sequences of nuclear ribosomal internal transcribed spacers (ITS), and implications for the classification of Rosoideae (Rosaceae). Pl. Syst. Evol. 211: 155–179.

Eriksson T., Hibbs M. S., Yoder A. D., Delwiche C. F., Donoghue M. J. (2003) The phylogeny of Rosoideae (Rosaceae) based on sequences of the internal transcribed spacers (ITS) of nuclear ribosomal DNA and the *trn*L/F region of chloroplast DNA. Int. J. Pl. Sci. 164: 197–211.

Evans R. C. (1999) Molecular, morphological, and ontogenetic evaluation of relationships and evolution in the Rosaceae. Ph.D. dissertation, University of Toronto, Toronto.

Evans R. C., Campbell C. S. (2002) The origin of the apple subfamily (Maloideae; Rosaceae) is clarified by DNA sequence data from duplicated GBSSI genes. Amer. J. Bot. 89: 1478–1484.

Evans R. C., Dickinson T. A. (1999a) Floral ontogeny and morphology in subfamily Amygdaloideae T. and G. (Rosaceae). Int. J. Pl. Sci. 160: 955–979.

Evans R. C., Dickinson T. A. (1999b) Floral ontogeny and morphology in subfamily Spiraeoideae Endl. (Rosaceae). Int. J. Pl. Sci. 160: 981–1012.

Evans R. C., Dickinson T. A. (2005) Floral ontogeny and morphology in *Gillenia* ("Spiraeoideae") and subfamily Maloideae C. Weber (Rosaceae). Int. J. Pl. Sci. 166: 427–447.

Evans R. C., Alice L. A., Campbell C. S., Kellogg E. A., Dickinson T. A. (2000) The granule-bound starch synthase (GBSSI) gene in the Rosaceae: multiple loci and phylogenetic utility. Molec. Phylogenet. Evol. 17: 388–400.

Farr D. F. (1989) Fungi on plants and plant products in the United States. APS Press, St. Paul, Minnesota.

Farr D. F., Rossman A. Y., Palm M. E., McCray E. B. (2005) Fungal databases, systematic botany and mycology laboratory. Agricultural Research Service, United States Department of Agriculture, available at http://nt.ars-grin.gov/fungaldatabases/.

Gladkova V. N. (1972) On the origin of subfamily Maloideae. Bot. Zhurn. 57: 42–49.

Gray A. (1842) The botanical text-book, ed. 1. Putnam, New York.

Greuter W., McNeil J., Barrie F. R., Burdet H. M., Demoulin V., Filgueiras T. S., Nicolson D. H., Silva P. C., Skog J. E., Trehane P., Turland N. J., Hawksworth D. L. (eds.) (2000) International code of botanical nomeclature. (Tokyo Code). Koeltz Scientific Books, Königstein.

Haruta M., Murata M., Hiraide A., Kadokura H., Yamasaki M., Sakuta M., Shimizu S., Homma S. (1998) Cloning genomic DNA encoding apple polyphenol oxidase and comparison of the gene product in *Escherichia coli* and in apple. Biosci. Biotechnol. Biochem. 62: 358–362.

Haruta M., Murata M., Kadokura H., Homma S. (1999) Immunological and molecular comparison of polyphenol oxidase in Rosaceae fruit trees. Phytochemistry 50: 1021–1025.

Helfgott D. M., Francisco-Ortega J, Santos-Guerra A., Jansen R. K., Simpson B. B. (2000) Biogeography and breeding system evolution of the woody *Bencomia* alliance (Rosaceae) in Macaronesia based on ITS sequence data. Syst. Bot. 25: 82–97.

Henrickson J. (1986) Notes on Rosaceae. Phytologia 60: 468.

Huelsenbeck J. P., Ronquist F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755.

Hutchinson J. (1964) The genera of flowering plants, vol. 1, Dicotyledons. Clarendon Press, Oxford.

Hutchinson J. (1969) Evolution and phylogeny of flowering plants. Academic Press, London.

International Plant Names Index (2006) Published on the internet at http://www.ipni.org.

Judd W. S., Olmstead R. G. (2004) A survey of tricolpate (eudicot) phylogenetic relationships. Amer. J. Bot. 91: 1627–1644.

Kalkman C. (1965) The Old World species of *Prunus* subgen. *Laurocerasus* including those formerly referred to *Pygeum*. Blumea 13: 1–115.

Kalkman C. (2004) Rosaceae. In: Kubitzki K. (ed.) The families and genera of vascular plants, vol. 6, Flowering plants - Dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales. Springer, Berlin, pp. 343–386.

Kerr M. S. (2004) A phylogenetic and biogeographic analysis of Sanguisorbeae (Rosaceae), with emphasis on the Pleistocene radiation of the high Andean genus *Polylepis*. Ph.D. dissertation, University of Maryland, College Park.

Koehne E. (1890) Die Gattungen der Pomaceen. Gaertner, Berlin.

Kubitzki K. (2004) The families and genera of vascular plants, vol. 6, Flowering plants – Dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales. Springer, Berlin.

Lawrence G. H. M. (1951) Taxonomy of vascular plants. Macmillan, New York.

Lee S., Wen J. (2001) A phylogenetic analysis of *Prunus* and the Amygdaloideae (Rosaceae) using ITS sequences of nuclear ribosomal DNA. Amer. J. Bot. 88: 150–160.

Mabberley D. J. (2002) *Potentilla* and *Fragaria* (Rosaceae) reunited. Telopea 9: 793–801.

Maddison, W. P., Maddison D. R. (2003) MacClade, version 4.06. Analysis of phylogeny and character evolution. Sinauer Associates, Inc., Sunderland, Massachusetts.

Missouri Botanical Garden (2005) Index to Plant Chromosome Numbers Database, available at http://mobot.mobot.org/W3T/Search/ipcn.html.

Morgan D. R., Soltis D. E., Robertson K. R. (1994) Systematic and evolutionary implications of *rbc*L sequence variation in Rosaceae. Amer. J. Bot. 81: 890–903.

Nylander J. A. A. (2005) MrAIC, version 1.4., available at http://www.abc.se/~nylander/.

Oh S. (2006) *Neillia* includes *Stephanandra* (Rosaceae). Novon 16: 91–95.

Oh S., Potter D. (2005) Molecular phylogenetic systematics and biogeography of tribe Neillieae (Rosaceae) using DNA sequences of cpDNA, rDNA, and *LEAFY*. Amer. J. Bot. 92: 179–192.

Oh S., Potter D. (2006) Description and phylogenetic position of a new angiosperm family, Guamatelaceae, inferred from chloroplast *rbc*L, *atp*B, and *mat*K sequences. Syst. Bot. 31: 730–738.

Pankhurst R. (2005) Rosaceae database. On-line searchable version available through the International Organization for Plant Information's Provisional Global Plant Checklist at: http://bgbm3.bgbm.fu-berlin.de/iopi/gpc/query.asp.

Potter D. (2003) Molecular phylogenetic studies in Rosaceae. In: Sharma A. K., Sharma A. (eds.) Plant genome: Biodiversity and evolution, vol. I, Pt. A: Phanerogams. Science Publishers, Inc. Enfield, New Hampshire, pp. 319–351.

Potter D., Gao F., Bortiri P. E., Oh S., Baggett S. (2002) Phylogenetic relationships in Rosaceae inferred from chloroplast *mat*K and *trn*L-*trn*F nucleotide sequence data. Pl. Syst. Evol. 231: 77–89.

Potter D., Still S. M., Ballian D., Kraigher H. (2006). Phylogenetic relationships in tribe Spiraeeae (Rosaceae) inferred from nucleotide sequence data. Pl. Syst. Evol. 266: 105–118.

Rambaut A. (1996) Se-Al: Sequence Alignment Editor. Available at http://evolve.zoo.ox.ac.uk/software.html.

Raspé O., Jacquemart A.-L., De Sloover J. (1998) Isozymes in *Sorbus aucuparia* (Rosaceae: Maloideae): genetic analysis and evolutionary significance of zymograms. Int. J. Pl. Sci. 159: 627–636.

Reveal J. L. (2004) Index nominum supragenericorum plantarum vascularum.?http://www.life.umd.edu/emeritus/reveal/pbio/WWW/supragen.html.

Robertson K. R., Phipps J. B., Rohrer J. R. (1991) A synopsis of genera in Maloideae (Rosaceae). Syst. Bot. 16: 376–394.

Rohrer J. R., Robertson K. R., Phipps J. B. (1994) Floral morphology of Maloideae (Rosaceae) and its systematic relevance. Amer. J. Bot. 81: 574–581.

Roitman A., Flaks B. R., Fradkina L. Z., Federov A. A. (1974) Chromosome numbers of flowering plants. Ger. Otto Koeltz Science Publishers, Koenigstein.

Savile D. B. O. (1979) Fungi as aids in higher plant classification. Bot. Rev. 45: 380–495.

Sax K. (1933) The origin of the Pomoideae. Proc. Amer. Soc. Hort. Sci. 30: 147–150.

Schulze-Menz G. K. (1964) Rosaceae. In: Melchior H. (ed.) Engler's Syllabus der Pflanzenfamilien II. 12th ed. Gebrüder Borntraeger, Berlin, pp. 209–218.

Shaw J., Small R. L. (2004) Addressing the "hardest puzzle in American pomology:" phylogeny of *Prunus* sect. *Prunocerasus* (Rosaceae) based on seven noncoding chloroplast DNA regions. Amer. J. Bot. 91: 985–996.

Simpson C .G., Macrae E., Gardner R. C. (1995) Cloning of a polygalacturonase inhibiting protein from kiwifruit (GenBank Z49063). Pl. Physiol. 108: 1748.

Smedmark J. E. E. (2006) Recircumscription of *Geum* L. (Colurieae: Rosaceae). Bot. Jahrb. Syst. 126: 409–417.

Smedmark J. E. E., Eriksson T. (2002) Phylogenetic relationships of *Geum* (Rosaceae) and relatives inferred from the nrITS and *trn*L-*trn*F regions. Syst. Bot. 27: 303–317.

Smedmark J. E. E., Eriksson T., Bremer B. (2005) Allopolyploid evolution in Geinae (Colurieae: Rosaceae) – building reticulate species trees from bifurcating gene trees. Organisms Divers. Evolut. 5: 275–283.

Smedmark J. E. E., Eriksson T., Evans, R. C. Campbell, C. S. (2003) Ancient allopolypoloid speciation in Geinae (Rosaceae): evidence from nuclear granule-bound starch synthase (GBSSI) gene sequences. Syst. Biol. 52: 374–385.

Soltis D. E., Soltis P. S., Chase M. W., Mort M. E., Albach D. C., Zanis M., Savolainen V., Hahn W. H., Hoot S. B., Fay M. F., Axtell M., Swensen S. M., Prince L. M., Kress W. J., Nixon K. C., Farris J. S. (2000) Angiosperm phylogeny inferred from 18S rDNA, *rbc*L, and *atp*B sequences. Bot. J. Linn. Soc. 133: 381–461.

Spjut R. W. (1994) A systematic treatment of fruit types. Mem. New York Bot. Gard. 70: 1–182.

Staden R. (1996) The Staden sequence analysis package. Mol. Biotechnol. 5: 233–241.

Sterling C. (1964) Comparative morphology of the carpel in the Rosaceae. III. Pomoideae: *Crataegus*, *Hesperomeles*, *Mespilus*, *Osteomeles*. Amer. J. Bot. 51: 705–712.

Sterling C. (1965a) Comparative morphology of the carpel in the Rosaceae. IV. Pomoideae: *Chamaemeles*, *Cotoneaster*, *Dichotomanthes*, *Pyracantha*. Amer. J. Bot. 52: 47–54.

Sterling C. (1965b) Comparative morphology of the carpel in the Rosaceae. V. Pomoideae: *Amelanchier*, *Aronia*, *Malacomeles*, *Malus*, *Peraphyllum*, *Pyrus*, *Sorbus*. Amer. J. Bot. 52: 418–426.

Sterling C. (1965c) Comparative morphology of the carpel in the Rosaceae. VI. Pomoideae: *Eriobotrya*, *Heteromeles*, *Photinia*, *Pourthiaea*, *Raphiolepis*, *Stranvaesia*. Amer. J. Bot. 52: 938–946.

Sterling C. (1966) Comparative morphology of the carpel in the Rosaceae. VII. Pomoideae: *Chaenomeles*, *Cydonia*, *Docynia*. Amer. J. Bot. 53: 225–231.

Stotz H. U., Powell A. L. T., Damon S. E., Greve L. C., Bennett A. B., Labavitch J. M. (1993) Molecular characterization of a polygalacturonase inhibitor from *Pyrus communis* L. cv. Bartlett. Pl. Physiol. (Lancaster) 102: 133–138.

Stotz H. U., Contos J. J., Powell A. L., Bennett A. B., Labavitch J. M. (1994) Structure and expression of an inhibitor of fungal polygalacturonases from tomato. Pl. Molec. Biol. 25: 607–617.

Swofford D. L. (2002) PAUP* Phylogenetic analysis using parsimony (* and other methods) Version 4. Sinauer Associates, Sunderland, Massachusetts.

Taberlet P., Gielly L., Patou G., Bouvet J. (1991) Universal primers for amplification of three noncoding regions of chloroplast DNA. Pl. Molec. Biol. 17: 1105–1109.

Takhtajan A. (1997) Diversity and classification of flowering plants. Columbia University Press, New York.

Thompson J. D., Gibson T. J., Plewniak F., Jeanmougin F., Higgins D. G. (1997) The CLUSTALX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucl. Acids Res. 25: 4876–4882.

Toubart P., Desiderio A., Salvi G., Cervone F., Daroda L., De Lorenzo G. (1992) Cloning and characterization of the gene encoding the endopolygalacturonase-inhibiting protein (PGIP) of *Phaseolus vulgaris* L. Pl. J. 2: 367–373.

Vanden Heuvel B. D., Benson D. R., Bortiri E., Potter D. (2004) Low genetic diversity among *Frankia* spp. strains nodulating sympatric populations of actinorhizal species of Rosaceae, *Ceanothus* (Rhamnaceae) and *Datisca glomerata* (Datiscaceae) west of the Sierra Nevada (California). Canad. J. Microbiol. 50: 989–1000.

Wallaart R. A. M. (1980) Distribution of sorbitol in Rosaceae. Phytochemistry 19: 2603–2610.

Weeden N., Lamb R. (1987) Genetics and linkage analysis of 19 isozyme loci in apple. J. Amer. Soc. Hort. Sci. 112: 865–872.

Wiens J. J. (2003) Missing data, incomplete taxa, and phylogenetic accuracy. Syst. Biol. 52: 528–538.

Xia X., Xie Z. (2001) DAMBE: software package for data analysis in molecular biology and evolution. J. Heredity 92: 371–373.

Yao C., Conway W. S., Sams C. E. (1995) Purification and characterization of a polygalacturonase-inhibiting protein from apple fruit. Phytopathology 85: 1373–1377.

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